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***Ambophthalmos* gen. nov. Diagnosed for
"Neophrynichthys" angustus and "N." magnicirrus,
and the Systematic Interrelationships of the Fathead
Sculpins (Cottoidei, Psychrolutidae)**

by

Keith L. Jackson



A thesis submitted to the Faculty of Graduate Studies and Research in
partial fulfilment of the requirements for the degree of
Masters of Science

Department of Zoology

Edmonton, Alberta

Spring 1996



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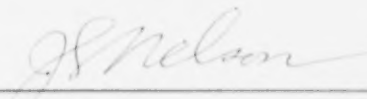
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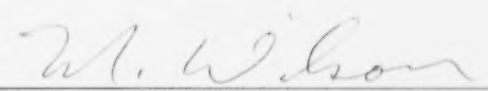
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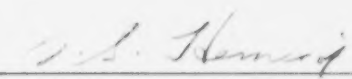
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Joseph S. Nelson



Mark V. H. Wilson



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29 Jan 1996

Abstract

"Neophrynichthys" angustus and *"N." magnicirrus* are two southern Pacific psychrolutids known not to belong in the genus *Neophrynichthys*, but of undetermined relationship. Detailed osteological study is presented on the family and especially on these two species. Parsimony analysis of anatomical characters was used to create a phylogenetic hypothesis of the family. Three synapomorphic characters suggest that *"N." angustus* and *"N." magnicirrus* form a monophyletic group. I diagnose *Ambophthalmos* gen. nov. for *A. angustus* and *A. magnicirrus*, as having the tabular bone of the pterotic fused anteriorly to the single supratemporal, supratemporal posteriorly fused to the posttemporal, and arch 2 medially fused to its antimere. Six characters suggest that *Cottunculus* is monophyletic and four synapomorphic characters suggest that *Ambophthalmos* is sister to *Cottunculus*. A cladistic classification of Psychrolutidae includes three new subfamilies, a redefined Cottunculinae, and an unchanged Psychrolutinae. These subfamilies are sequenced as Dasycottinae, Eurymeninae, Cottunculinae, Malacocottinae, and Psychrolutinae.

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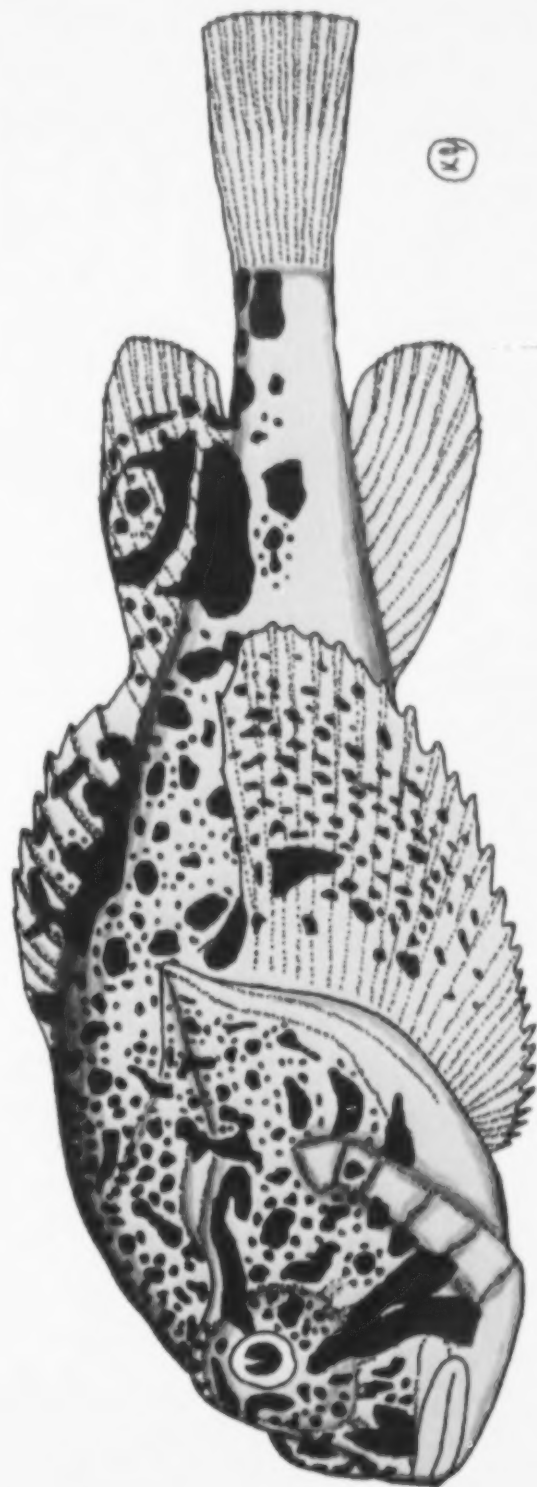
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Ambophthalmos angustus

Introduction

Nelson (1977) described *Neophrynychthys angustus* and *N. magnicirrus*, but considered their generic placement as uncertain and needing further investigation. Their placement in *Neophrynychthys* was put in further doubt when Nelson (1982) divided Psychrolutidae into two subfamilies, each distinguished by the condition of the interorbital region of the skull. The genus *Neophrynychthys* was placed in the subfamily Psychrolutinae because the type species (*N. latus*) has a weak interorbital region, the diagnostic character of that subfamily. *N. angustus* and *N. magnicirrus* have a rigid interorbital region, characteristic of the subfamily Cottunculinae. They were placed in Cottunculinae as "genus undescribed" by Nelson (1982:1480) with *Neophrynychthys* being placed in quotation marks indicating that the two species probably do not belong in this genus; Nelson suggested that more study be done to resolve the problem. Since then, the systematics of these two species have not been examined, and their formal generic placement remains unresolved.

The objective of this study is to provide a better understanding of the relationships of "*Neophrynychthys*" *angustus* and "*N.*" *magnicirrus* within the Psychrolutidae. Detailed osteological study was done on representative psychrolutid fishes with emphasis on the two species in question. Anatomical homologies were used to estimate the interrelationships of Psychrolutidae. Parsimony analysis of anatomical characters was used to create a phylogenetic hypothesis of the family. A cladistic classification of generic relationships is presented to provide a more informative nomenclatorial system for Psychrolutidae. The evolution and biogeography of these two species is discussed.

I establish *Ambophthalmos* gen. nov., for "*Neophrynichthys*" *angustus* and "*N.*" *magnicirrus*. This new classification is followed here, except in historical references to these fish.

A Short History of Psychrolutid Systematics

Günther (1861) established the family Psychrolutidae for *Psychrolutes paradoxus*, described from a single specimen collected from the Gulf of Georgia, Vancouver Island. Günther (1861) suggested that *P. paradoxus* has a "natural affinity" with the Discoboli and Gobiesoces (presently the Liparidae and Gobiesocidae). Since Günther's early work, the family has been variously classified within the Cottoidei, and seven genera including about 29 species are currently assigned to the family (Nelson, 1994). The composition and classification of the Psychrolutidae have varied since it was established. I will discuss the history of the family's classification in chronological order, starting after Günther (1861) and extending to the most recent classification (Nelson, 1994).

Kner (1868) described *Bunocottus apus* from Cape Horn and assigned it to the Cottina (presently Cottidae). This fish may be the second described psychrolutid, as Nelson and Nakamura (1980) believe it may be synonymous with *Cottunculus granulatus* Karrer, 1968. The second undisputed psychrolutid described is *Cottunculus microps* Collett, 1875 from the North Atlantic, west of Spitzbergen. This fish was originally assigned to the Cottina. Collett (1880) suggested that *Cottunculus microps* is not closely related to any other Arctic cottid; however pectoral and pelvic girdles, teeth, and general body shape are

similar to that of cottids.

The third described psychrolutid, and second to be assigned to this family, is *Psychrolutes latus* Hutton, 1875 from New Zealand waters. Günther (1876) examined the holotype of *P. latus* and concluded that it belongs in its own genus, for which *Neophrynichthys* was erected in the family Psychrolutidae. It was thought, correctly, that *N. latus* had a spinous dorsal fin and, incorrectly, that *P. paradoxus* lacked it. It was later shown that *P. paradoxus* has a small spinous dorsal fin (Jordan and Gilbert, 1883). Despite this oversight that resulted in its separation from *Psychrolutes*, *N. latus* was found to be distinct in other characters, and *Neophrynichthys* was retained (Gill, 1888) (for a current diagnosis and discussion of the history of the nominal genus *Neophrynichthys* and family Neophrynichthyidae, see Nelson (1977)). Five years after *N. latus* was described from New Zealand, Günther (1881) reported a similar fish collected from the Straits of Magellan and off the Patagonian coast. Gill (1888) reexamined Günther's specimens, concluded that the South American fish was distinct, and named it *N. marmoratus*. *Besnardia gyrinops* Lahille, 1913 was considered a junior synonym of *N. marmoratus* by Norman (1937).

Bean (1890) described *Dasycottus setiger*, *Malacocottus zonurus*, and *Psychrolutes zebra* from Alaskan waters. He suggested that *Dasycottus* is probably related to *Cottunculus* and noted the similarity in shape between *Malacocottus* and *Cottunculus* species. Bean (1890) did not speculate on the relationship of *Psychrolutes*; however, an earlier paper suggested *Cottunculus* and *Psychrolutes* to be closely related (Jordan and Gilbert, 1883).

Gilbertina sigalutes Jordan and Starks, 1895 was described from Puget Sound. The genus *Gilbertina* was the fifth genus placed in Psychrolutidae. Berg (1898) changed the generic nomen to *Gilbertidia* due to its conflict with a previously named mollusc. This genus remained until Nelson (1982) gave evidence for close a relationship to *Psychrolutes paradoxus* and considered *Gilbertidia* to be a junior synonym of *Psychrolutes*.

Jordan and Everman (1898) classified all known North American cottoids. *Cottunculus*, *Dasycottus*, and *Malacocottus* were placed in the Cottinae, *Gilbertidia* and *Psychrolutes* in the Psychrolutinae, with both subfamilies in Cottidae. Psychrolutinae was suggested to be close to *Cottunculus* and *Malacocottus* (Jordan and Everman, 1898).

The last two currently recognised genera to be established were *Eurymen* (for *E. gyrinus* Gilbert and Burke 1912) and *Ebinania* (for *E. vermiculata* Sakamoto, 1932). Barnard (1927) erected the genus *Cottunculoides* (for *C. inermis* and *C. spinosus*), and distinguished it from *Cottunculus* by absence of vomerine teeth. However, *Cottunculoides* was reduced to subgenus in *Psychrolutes* (Nelson, 1982).

Two species in two monotypic genera have been described that may be psychrolutids, but neither is currently recognised. Smith (1904) described *Thecopterus aleuticus* from the Bering Sea, diagrammed it, and discussed its similarity to *Dasycottus* and *Malacocottus*. The holotype and only known specimen has been lost, and new material has not been found (Nelson, 1982). Lloyd (1909) described *Liparoides beauchampi* from the Bay of Bengal and Stein (1978) provided reason to believe that this fish is probably a cottid, perhaps similar to *Cottunculus*. The holotype was also

lost, but new material would be of interest as the north Indian Ocean has not produced any psychrolutids.

The remaining history of psychrolutid systematics involves new species descriptions and shifting species between genera and genera between Psychrolutidae and other cottoid families and subfamilies. Regan (1913) removed the Cottunculidae and Psychrolutidae from Cottidae. Jordan (1923) divided the group further by separating Neophrynichthyidae (see Nelson, 1977, for a discussion of the history of this taxon) from Psychrolutidae. It was not until Taranets (1941) that all seven genera (at that time ten, including *Cottunculoides*, *Thecopterus*, and *Gilbertidia*) were included in the family Psychrolutidae. The family was diagnosed as having no more than 20 lateral line pores and always seven branchiostegal rays (Taranets, 1941).

Nelson (1982) divided the family into two subfamilies, Psychrolutinae and Cottunculinae, each diagnosed by the condition of the interorbital region of the skull. In psychrolutines the interorbital region is wide and weakly ossified while in cottunculines it is narrow and rigid. *Cottunculus*, *Dasycottus*, *Eurymen*, and *Malacocottus* spp. were placed in the Cottunculidae. *Ebinania*, *Neophrynichthys*, and *Psychrolutes* were placed in the Psychrolutinae. Based on condition of the interorbital region, two species were reassigned from *Cottunculus* to *Ebinania* and two former species of *Neophrynichthys*, *N. angustus* and *N. magnicirrus*, were placed in the subfamily Cottunculinae, genus undescribed. The nominal genus *Cottunculoides* was reduced to a subgenus in *Psychrolutes*. *Gilbertidia sigalutes* was placed in the subgenus *Psychrolutes* and *Gilbertidia* was considered a junior synonym of *Psychrolutes*. Nelson's

(1982) revision of psychrolutid classification is reflected in Nelson (1994), the most recent account of the classification of Psychrolutidae. Table 1 lists all currently recognised psychrolutids.

Psychrolutidae are a monophyletic group is defined by several morphological characters. Yabe (1985) recognised two synapomorphic characters supporting psychrolutid monophyly: connection of the operculomandibular sensory canal to the infraorbital sensory canal and absence of pores between actinosts. Nelson (1982) diagnosed psychrolutids as having cranial sensory canals enlarged and exposed, and supported by thin, bony arches. The first two characters are unique to Psychrolutidae within the suborder Cottoidei and the last character is unique to Psychrolutidae within the superfamily Cottoidea.

Although psychrolutids are a natural group, their position within the Cottoidei is not certain. Traditionally, the family was thought to contain "degraded" cottids; some authors even placed psychrolutid genera in the subfamily Cottinae (e.g., Jordan and Starks, 1903). Evidence now suggests a more basal split from other Cottoidea (Figure 1). However, this phylogeny may not be stable because Yabe (1985) used only seven characters to support it. Higher level relationships are better resolved. Yabe (1985) listed 22 synapomorphic characters uniting the Cottoidea. Shinohara (1994) listed three synapomorphic characters for Cottoidei and six synapomorphic characters suggesting a sister group relationship with the monophyletic group formed by *Hexagrammus*, *Ophiodon*, and *Pleurogrammus* (Hexagrammidae).

Yabe (1985) examined osteology and myology of representatives of the superfamily Cottoidea to infer its phylogeny. Although his study was

Table 1. Psychrolutid classification sensu 1995. Types are indicated in bold. Subgenera given in parentheses.

Psychrolutidae

Cottunculinae

<i>Cottunculus granulosus</i>	Karrer, 1968
<i>Cottunculus microps</i>	Collette, 1875
<i>Cottunculus nudus</i>	Nelson, 1989
<i>Cottunculus sadko</i>	Essipov, 1937
<i>Cottunculus thomsonii</i>	(Günther, 1882)
<i>Dasycottus setiger</i>	Bean, 1890
<i>Eurymen gyrinus</i>	Gilbert and Burke, 1912
<i>Malacocottus gibber</i>	Sakamoto, 1930
<i>Malacocottus kincaidi</i>	Gilbert and Thompson, 1905
<i>Malacocottus zonurus</i>	Bean, 1890
" <i>Neophrynichthys</i> " <i>angustus</i>	Nelson, 1977
" <i>Neophrynichthys</i> " <i>magnicirrus</i>	Nelson, 1977

Psychrolutinae

<i>Ebinania brephocephala</i>	(Jordan and Starks, 1903)
<i>Ebinania costaecanarie</i>	(Cervignon, 1961)
<i>Ebinania malacocephala</i>	Nelson, 1982
<i>Ebinania macqariensis</i>	Nelson, 1982
<i>Ebinania vermiculata</i>	Sakamoto, 1932
<i>Neophrynichthys latus</i>	(Hutton, 1875)
<i>Neophrynichthys marmoratus</i>	Gill, 1889

Psychrolutes

(<i>Cottunculoides</i>) <i>inermis</i>	(Vaillant, 1888)
(<i>Cottunculoides</i>) <i>macrocephalus</i>	(Gilchrist, 1904)
(<i>Cottunculoides</i>) <i>marcidus</i>	(McCulloch, 1926)
(<i>Cottunculoides</i>) <i>occidentalis</i>	Fricke, 1986
(<i>Cottunculoides</i>) <i>phrictus</i>	Stein and Bond, 1978
(<i>Cottunculoides</i>) <i>sio</i>	Nelson, 1980
(<i>Cottunculoides</i>) <i>subspinosus</i>	(Jensen, 1902)
(<i>Psychrolutes</i>) <i>paradoxus</i>	Günther, 1861
(<i>Psychrolutes</i>) <i>pustulosa</i>	(Schmidt, 1937)
(<i>Psychrolutes</i>) <i>sigalutes</i>	(Jordan and Starks, 1895)

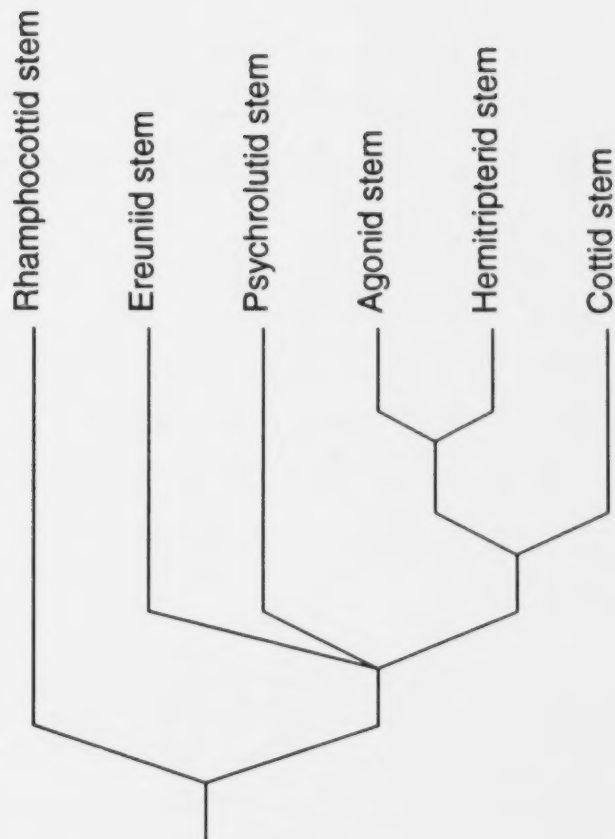


Figure 1. Phylogeny of the Cottoidea (after Yabe, 1985).

wide in scope, he managed to examine members of at least one species of all seven psychrolutid genera (as per Nelson, 1982). Yabe (1985) found five informative characters within the psychrolutids and two synapomorphies unique to the family. The phylogeny he derived is shown in Figure 2. This phylogeny disagrees with Nelson's (1982) synthetic classification, in which he believes there to be two natural groups within Psychrolutidae. If Yabe's phylogeny is correct, Cottunculinae would be paraphyletic and Psychrolutinae not monophyletic without inclusion of *Malacocottus*. However, only seven characters of Yabe's study were significant in interpreting the phylogeny of Psychrolutidae. Yabe (1985) did not propose a new classification.

Distribution and Ecology

Psychrolutids have a wide geographic distribution, typically associated with cool to cold waters (Figure 3). In cool temperate regions, some species may be taken from shallow water. In tropical waters, the few species represented are found in deep water, to 2800 m. In contrast to most other cottoid families that are most diverse in the Northern Hemisphere, psychrolutids are evenly distributed. The genera *Dasycottus*, *Malacocottus*, and *Eurymen*, the most generalised and presumably most primitive members of the family, are found in the north Pacific. This agrees with the hypothesis of this region being the centre of origin of the Cottoidea. *Cottunculus*, *Ebinania*, and *Psychrolutes* have members in both the northern and southern hemispheres. *Neophrynichthys* is found only in New Zealand and southern South American waters. "*Neophrynichthys*" *angustus* and "*N.*" *magnicirrus* are found in New

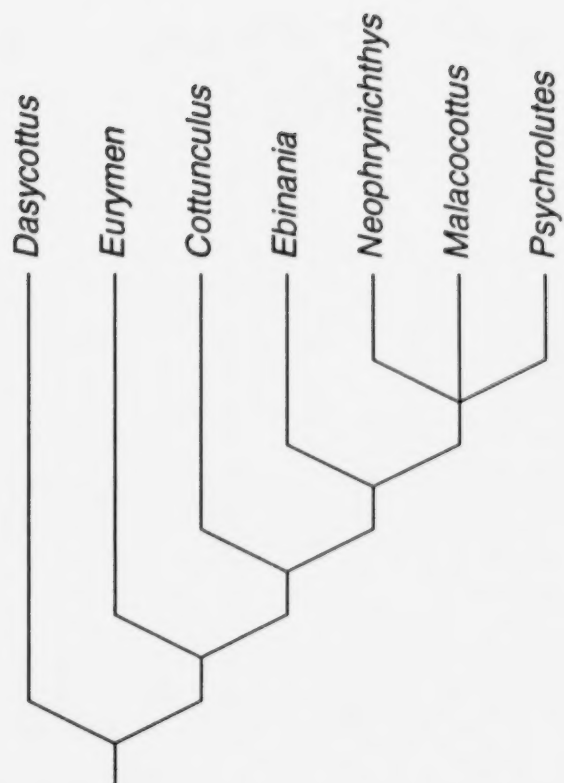


Figure 2. Phylogeny of psychrolutid genera (after Yabe, 1985).

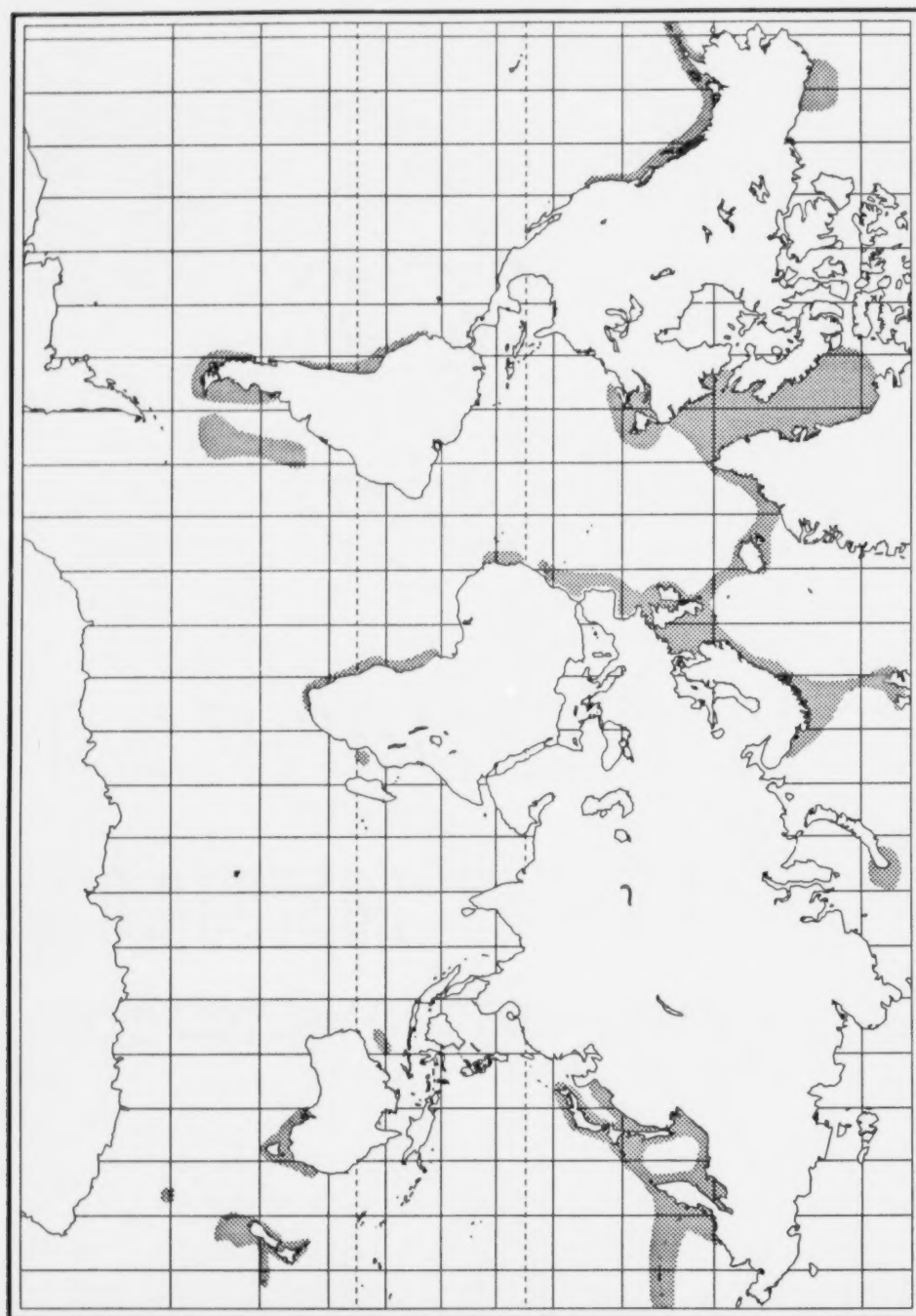


Figure 3. Distribution of Psychrolutidae

Zealand and Macqarie Island (54° S, 159° E) waters, respectively.

All species are generally tadpole shaped, the head being round and globular with the body tapering to a small tail. The mouth is very large and stomach contents indicate an omnivorous diet. *Neophrynichthys latus* buries itself in the sand with only its mouth and eyes exposed, engulfing a passing crab or flounder with its massive mouth (Graham, 1956). Notes on reproduction and feeding can be found in Graham (1939a) and Graham (1939b). Due to inaccessibility and low economic value of these fish, no modern ecological studies have been published on these enigmatic deep water fishes.

Materials and Methods

Specimens and Notes

Institutional abbreviations follow Levinton et al. (1985). Three fields of information are given in parentheses for each specimen or lot of specimens. Specimens per lot is in the first field. Standard length (SL), given to the nearest millimetre, is in the next field. The last field describes specimen preparation and notes. Whole specimens are indicated as "alcohol prep.", and may have some anatomy dissected. Specimens or structures cleared and stained for osteology are indicated as CS. Specimens or structures cleared and counter stained for osteology and cartilage are indicated as CCS. Clearing and staining follows Taylor (1967) or Taylor and Van Dyke (1985). Specimens examined include:

Psychrolutidae: *Cottunculus thomsonii*: UAMZ 4526 (1; 355 SL; alcohol prep.). UAMZ 4527 (1; 170 SL; alcohol prep.). UAMZ 4528 (1; 176 SL; cranium extracted and stained with alizarin; pectoral/pelvic girdle and caudal skeleton removed and CCS). UAMZ 6493 (1; 182 SL; alcohol prep.). *Dasycottus setiger*: UAMZ 749 (5; 83-102 SL; alcohol prep.). UAMZ 1973 (7; 62-135 SL; alcohol prep.). UAMZ 2390 (1; pectoral girdle/pelvic girdle extracted and CCS). UAMZ 3181.4 (2; approx. 100 SL; CS). UAMZ 3196.5 (3; 74-83 SL; CS; hyoid apparatus extracted from one). *Ebinania brephocephala*: HUMZ 51823 (1; 116 SL; alcohol prep.). HUMZ 52187 (1; 113 SL; CS). *Eurymen gyrinus*: HUMZ 68060 (1; 132 SL; CS). HUMZ 124703 (1; 265 SL; alcohol prep.). *Malacocottus gibber*: HUMZ 109404 (1; 141 SL; CS). HUMZ 109971 (1; 135 SL; alcohol prep.). *Malacocottus kincaidi*: UAMZ 3186.7 (3; 42-49 SL; alcohol prep.). UAMZ 4497 (10; 41-55 SL; 4 alcohol prep., 1 CCS, 5 CS hyoid apparatus extracted from one).

Ambophthalmos angustus ("Neophrynychthys" *angustus*): FAKU 46748 (1; 290 SL; alcohol prep.). FAKU 47077 (1; 235 SL; pectoral/pelvic girdle extracted and CCS). NMNZ P. 6339 (2 of 4; 107-210 SL; alcohol prep.). NMNZ P. 6579 (2 of 4; 143-250 SL; alcohol prep.). NMNZ P. 6889 (4 of 9; 111-187 SL; alcohol prep.). NMNZ P. 21416 (1; 64 SL; CCS). NMNZ P. 27002 (1 of 3; 350-380 SL; alcohol prep.). *Ambophthalmos magnicirrus* ("Neophrynychthys" *magnicirrus*): LACM 10983-2 (1 of 3; 200-250 SL; alcohol prep.; paratype). *Neophrynychthys latus*: UAMZ 7598 (2; 176 and unknown SL; head, pectoral/pelvic girdle, and caudal skeleton of one extracted and CCS). *Psychrolutes paradoxus*: UAMZ 2778 (1; 34 SL; CCS). UAMZ 3195 (1; 36 SL; alcohol prep.). UAMZ 4618 (2; 36 and 37 SL; CS; hyoid apparatus extracted from one). *Psychrolutes phrictus*: LACM 35770-1 (2; 538 SL; osteological prep.). UAMZ 4496 (2; 355 and 460 SL; alcohol prep.). *Psychrolutes sigalutes*: UAMZ 1288 (9; 38-41 SL; alcohol prep.). UAMZ 1976 (2 ; 37 and 41 SL; CS).

Cottidae: *Cottus ricei*: UAMZ 2576 (3; 46-89 SL; CS). UAMZ 7622 (4; 59-68; alcohol prep.). *Jordania zonope*: UAMZ 1058 (2; approx. 71 and 81 SL; CS). UAMZ 1560 (5; 54-59 SL; alcohol prep.).

Hexagrammidae: *Hexagrammus stelleri*: UAMZ 2329 (4; 52-76 SL; alcohol prep.). UAMZ 2355 (3; 45-52 SL; CS).

Diagrams were drawn with the aid of a drawing tube on a Wild M5 stereo dissecting scope or photographs taken with a 35 mm SLR camera and closeup lens. Drawings were scanned with an Apple OneScanner for editing and composition by computer. All figures are by the author unless noted otherwise.

Selection of Study Group

Outgroup comparison is used to determine character polarity. The ingroup used is Psychrolutidae, since the objective of this study is to clarify the relationship of *Amblophthalmos angustus* and *A. magnicirrus* within this family. The outgroups selected for polarising characters in the ingroup are the cottids *Cottus ricei* and *Jordania zonope*, and the hexagrammid *Hexagrammus stelleri*.

Basal relationships of the Cottoidei are poorly resolved, and the sister group to the Psychrolutidae is not established. Yabe's (1985) cottoid phylogeny shows a polychotomy between Ereuniidae, Psychrolutidae, and a monophyletic group comprising Agonidae, Cottidae, and Hemitriptidae (Figure 1). The cottoid outgroups used here may not be in the sister group of the Psychrolutidae; however, they are generalised cottoids and likely show primitive states for most characters examined. A hexagrammid was chosen to compare character states in a more distantly related taxon. Quast (1965) argued that hexagrammids are primitive cottoids and should be placed in that suborder. Shinohara (1994) found Hexagrammidae to be paraphyletic without the inclusion of Cottoidei; *Hexagrammus*, *Ophiodon*, and *Pleurogrammus* form a monophyletic group sister to Cottoidei as supported by six synapomorphic characters. Although *Hexagrammus* is specialized in its own right, it does show good examples of primitive cottoid anatomy.

At least one specimen from each valid genus of psychrolutids was selected for analysis of character states (Table 2). Literature was reviewed for determining character states in *Cottunculus granulosus* (primarily Nelson and Nakamura (1980), for their detailed anatomical descriptions).

Each species was treated as a terminal taxon in parsimony analysis. Each genus is assumed to be monophyletic so that generic relationships are reflected in the phylogenetic hypothesis of specific relationships. When possible, literature was reviewed to determine consistency of characters in other species of each genus. Inconsistencies were few and are discussed in the character description section.

Table 2. Study group (alphabetical order).

Outgroup

Cottus ricei
Hexagrammus stelleri
Jordania zonope

Ingroup

Ambophthalmos angustus
Ambophthalmos magnicirrus
Cottunculus granulatus
Cottunculus thomsonii
Dasycottus setiger
Ebinania brephocephala
Eurymen gyrinus
Malacocottus gibber
Malacocottus kincaidi
Neophrynichthys latus
Psychrolutes phrictus
Psychrolutes paradoxus
Psychrolutes sigalutes

Results

Characters Examined

Thirty-seven characters are examined to interpret the phylogeny of Psychrolutidae. Cranial osteology (Figures 4, 5, and 6) accounts for twenty-four characters examined. The first six cranial characters (1-6) are from general cranial osteology. The remaining eighteen cranial characters (7-24) are from a functional group, the cranial sensory canal system and related osteology. Eight characters (24-31) are from the pectoral and pelvic girdles (Figures 7 and 8). Two characters (32 and 33) are from the caudal skeleton (Figure 9). The remaining four characters are from myology and the integument. A summary of characters and states described below is given in Appendix 1. A summary of character distribution among the taxa examined is given in Appendix 2.

Cranial Osteology

1. Vomerine teeth (prevomer of Nelson, 1982) — The vomer may possess teeth or lack them (states 0 and 1 respectively). Specimens of the outgroups, *Dasycottus*, *Eurymen*, and *Cottunculus*, have a toothed vomer. Adult specimens of *Ambophthalmos*, *Malacocottus*, *Neophrynichthys*, and *Psychrolutes* lack teeth on the vomer.
2. Skull roof — The skull roof is formed primarily by the epiotics, exoccipitals, frontals, parietals, pterotics, and supraoccipital. Two conditions of the skull roof are observed. Specimens of the outgroups, *Ambophthalmos*, *Cottunculus*, *Dasycottus*, *Eurymen*, and *Malacocottus*, have a well ossified and rigid skull roof (state 0) while those of *Ebinania*, *Neophrynichthys*, and *Psychrolutes* have a soft weakly ossified skull roof

(state 1). The frontals show the greatest contrast between these two states.

3&4. Orbital ridge — I define the orbital ridge as the dorsal rim of the orbit formed by the lateral edge of the frontal. A crease identifies this ridge as a distinct part of the frontal. *Ambophthalmos* specimens have the most developed orbital ridge, being thick and high. *Cottunculus* specimens have the next most well developed ridge, followed by those of *Dasycottus*, *Malacocottus*, and the outgroups. *Ebinania*, *Neophrynichthys*, and *Psychrolutes* fish have a very thin orbital ridge that extends over the eye, greatly increasing the interorbital distance. The first character (3) of the orbital ridge is either normal (state 0) or a thin sheet forming an extended dorsal wall of the orbit (state 1).

Inclusion of the sphenotic in the orbital ridge is the second character (4). The sphenotic forms the posterodorsal wall of the orbit and has a small dorsal exposure confined to the posterior corner of the orbit, where it forms a groove articulating with the last infraorbital. In the outgroups and in psychrolutids other than *Ambophthalmos* and *Cottunculus*, the sphenotic does not contribute to the orbital ridge (state 0). In specimens of these two genera, the posterior end of the orbital ridge extends laterally and includes the sphenotic (state 1).

5. Sphenotic — This is a binary character. The normal state (0) is for the sphenotic groove (articulation point for the last infraorbital) to not be pronounced. In the specialized state (1), seen in *Psychrolutes paradoxus* and *P. sigalutes*, the sphenotic groove is borne on a lateral extension of the sphenotic. This is the "two pronged autosphenotic" of Nelson (1982).

6. Subopercle (SOP) — This is a binary character. The normal condition of

this bone is a broad blade-like form (state 0). The specialized condition, seen in *Psychrolutes paradoxus* and *P. sigalutes*, is long and rod-like (state 1).

Cranial Canals and Associated Osteology

Psychrolutids have a specialized, cranial sensory canal system. Most canals are greatly enlarged and traverse in grooves on the surface of the skull (Figure 4). In comparison, cottids and most other cottoids have relatively narrow canals completely covered by skull roofing bones with small openings allowing passage of sensory pores. In psychrolutids this bony covering is reduced to thin arches (Figure 5). These arches are comparable between psychrolutids and homologies are not difficult to ascertain. This, coupled with significant interspecific variation, provides a wealth of phylogenetically significant characters. Eighteen characters (7-24) were described of the cranial canal system and associated osteology.

Nelson (1982) described these arches and provided a system for their identification. The arches are numbered anteriorly to posteriorly from one to six (A1-A6). Arches 1-4 are borne on the frontal and they rim the orbit. The supraorbital canal (STC) is supported by arches 1-4. Arch 5 is borne on the pterotic and supports the anterior extension of the supratemporal canal. Arch 6 is borne on the parietal and supports the medial portion of the supratemporal canal. The supratemporal canal is supported by arch 5, arch 6, an arch borne on the posttemporal, a tabular bone of the pterotic, and one to three supratemporals. *Eurymen* specimens have three supratemporals, those of *Dasycottus* have two, and all other psychrolutids have one. Two supratemporals is the primitive condition for

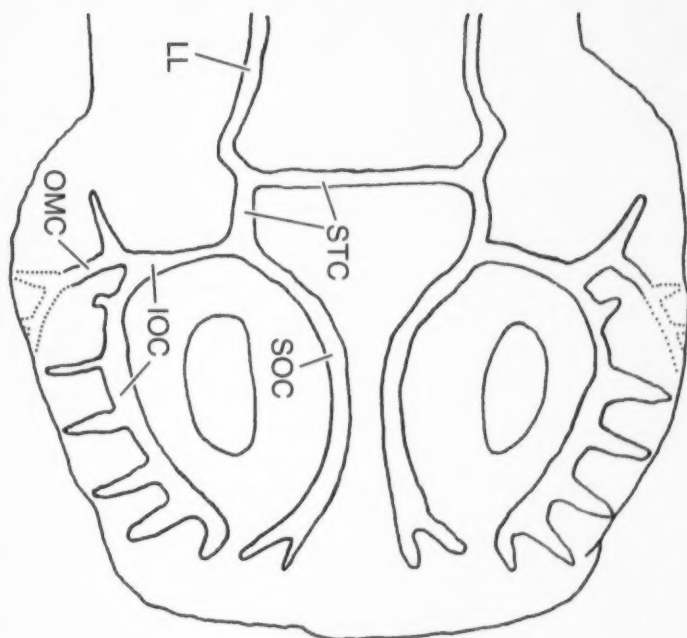


Figure 4. Cranial canal system of *Ambloptalmos angustus* in dorsal aspect. IOC, infraorbital canal; LL, lateral line; OMC, operculomandibular canal; SOC, supraorbital canal; STC, supratemporal canal.

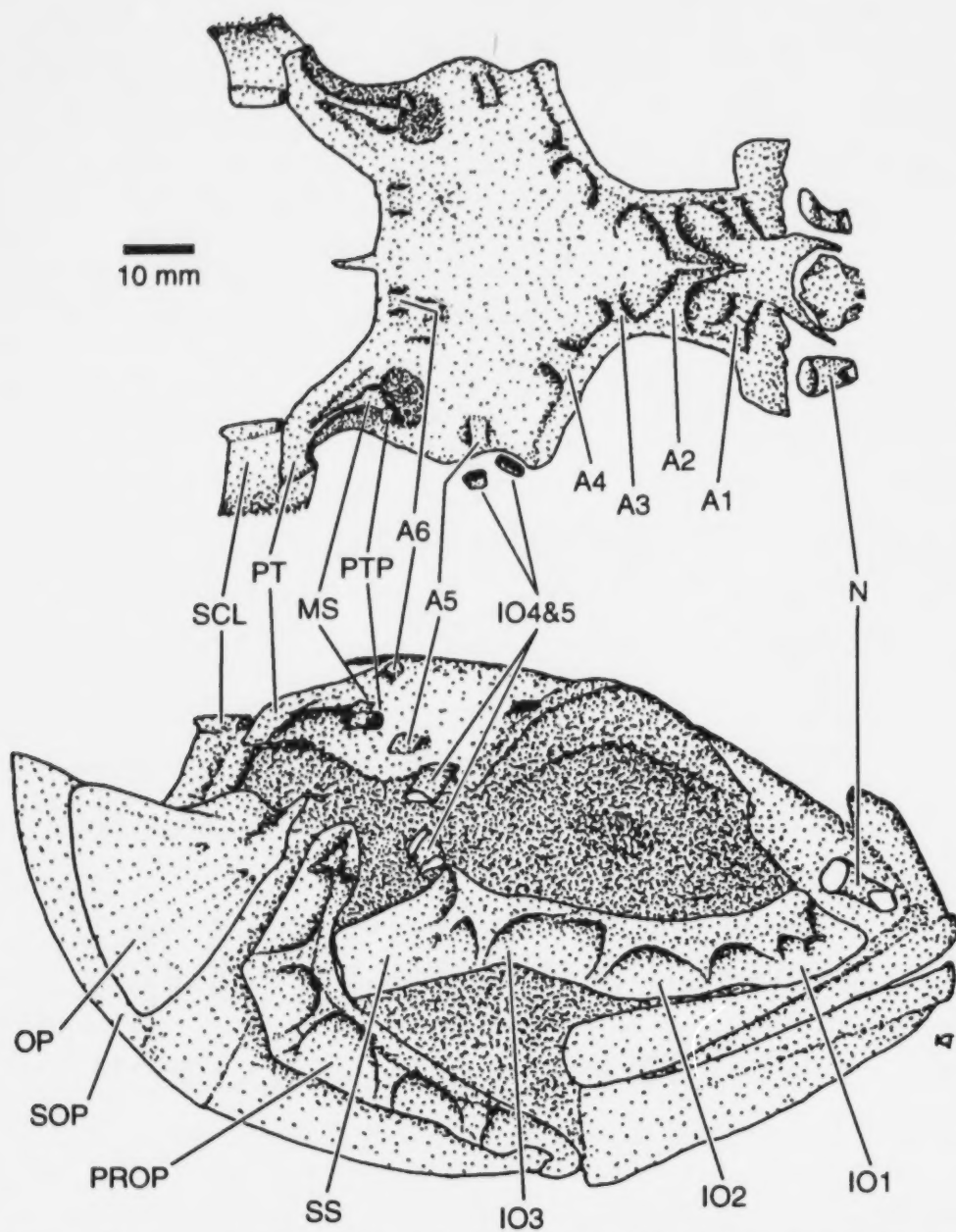


Figure 5a. Superficial cranial osteology of *Ambloptalmos angustus*. Top diagram in dorsal aspect, bottom in lateral aspect. A1-A6, cranial arches 1-6; IO1-5, infraorbitals 1-5; MS, medial supratemporal; N, nasal; OP, opercle; PROP, preopercle; PT, posttemporal; PTP, posterior tabular bone of the pterotic; SCL, supracleithrum; SOP, subopercle; SS, suborbital (infraorbital) stay.

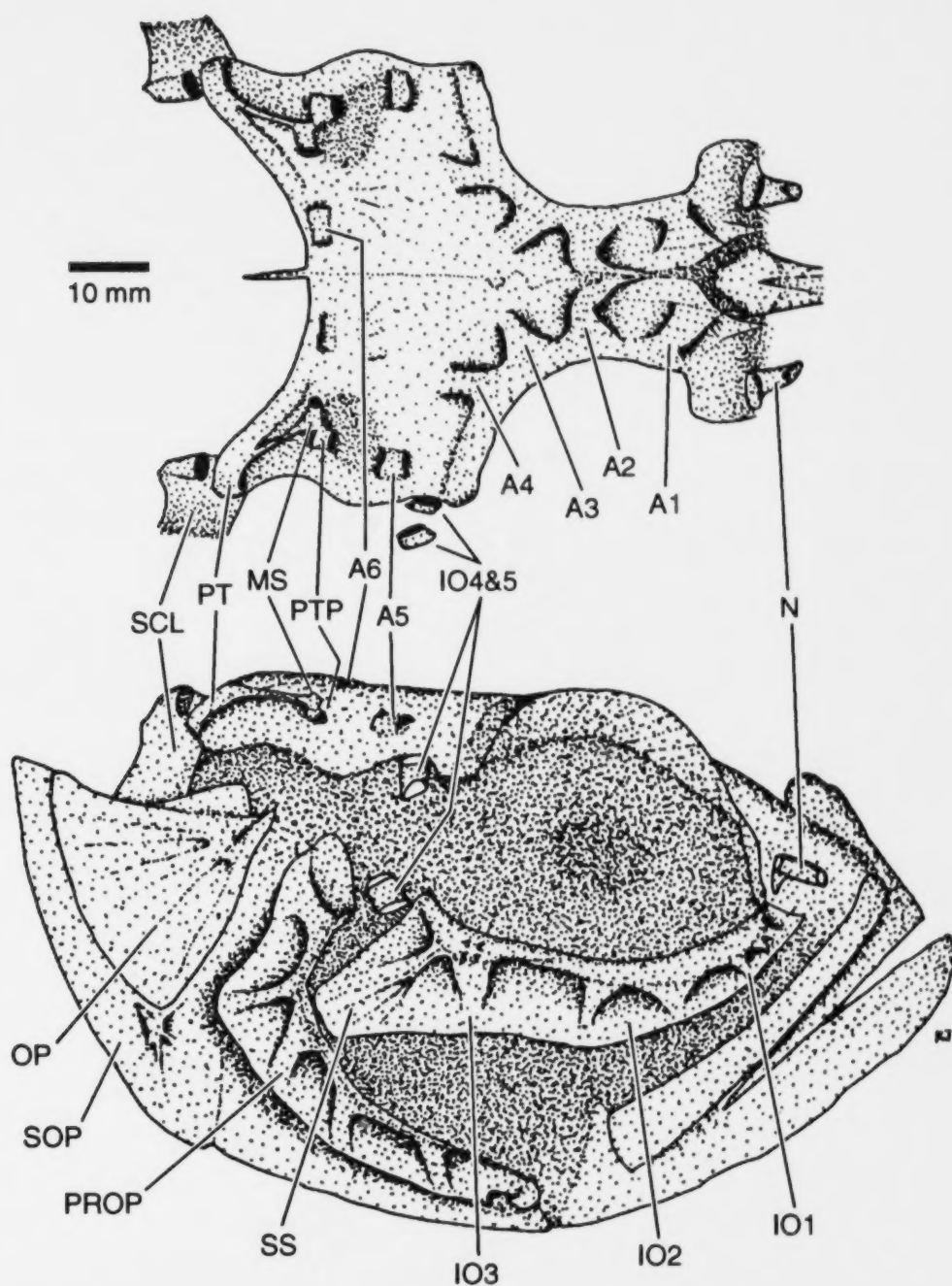


Figure 5b. Superficial cranial osteology of *Ambloptalmos magnicirrus*. Top diagram in dorsal aspect, bottom in lateral aspect. Abbreviations given in Figure 5a.

psychrolutids (Yabe, 1985). Nelson (1982) termed the supratemporals and tabular bone of the pterotic as "tabulars". I follow Yabe's (1985) terminology, as he showed the anterior "tabular" of Nelson to originate from an arch on the pterotic, whereas Nelson's posterior and medial "tabulars" are supratemporal bones associated with the pectoral girdle.

The infraorbital canal (IOC) originates on the dorsal exposure of the sphenotic at the junction of the supraorbital and supratemporal canal. Infraorbitals 4 and 5 (IO4-IO5) (postorbitals) are simple tubular bones supporting the posterior portion of the infraorbital canal. Infraorbitals 1-3 (IO1-IO3) (lachrymal and suborbitals) form a flat plate-like suborbital bar. Each suborbital possesses two arches supporting the infraorbital canal. *Psychrolutes sigalutes* has only one arch on the third infraorbital, but two are present on infraorbitals 1 and 2. The opercular (operculomandibular) canal (OMC) joins the infraorbital canal between infraorbitals 4 and 5, and follows the curvature of the preopercle (PROP) to connect with the mandibular canal. Five arches are present on the preopercle.

Cottunculus, *Dasycottus*, and *Malacocottus* spp. have spines borne high on some to most of their arches. *Cottunculus* specimens have the best developed spines (although there is variation between species, Nelson, 1989). The cranial, infraorbital 1-3, posttemporal, preopercular, tabular, and supratemporal arches bear well developed spines. Specimens of *Dasycottus* have well developed spines on cranial, posttemporal, tabular, and supratemporal arches, but only small ones on the preopercular arches, and none on the the infraorbital arches. Those of *Malacocottus* have only minute spines on two preopercular arches; all

other cranial and infraorbital arches are spineless.

7. Cranial sensory canals — This character is binary. In all cottoid fishes excluding psychrolutids, bone extensively covers the sensory canals (state 0). In all psychrolutids, this bone covering is reduced to thin arches (state 1) (Nelson, 1982). Also, diameter of psychrolutid cranial canals is considerably wider than in other scorpaeniforms, resulting in the arches being high and conspicuous (Figure 5). The infraorbital and preopercular arches are also more developed in psychrolutids than in other cottoids.

8. Spines on cranial arches — This character is binary. Absence of spines (state 0) is the condition in non-psychrolutid cottoids and members of several psychrolutid genera. Although non-psychrolutids have bone covering their cranial canals rather than arches, spines are never found on bone over the canals. The cottid *Myoxocephalus quadricornis* has spines on its head, but not on bone covering the cranial canals (Nelson, 1982). Species of the psychrolutid genera *Dasycottus* and *Cottunculus* have well developed spines or blunt protuberances borne high on all cranial arches (state 1).

9. Arch 2-3 (A2-A3) — This character is binary. In *Dasycottus* fish, Arches 2 and 3 are partly fused laterally forming a ridge that partly covers the supraorbital canal (state 0). In *Ambophthalmos*, *Cottunculus*, and *Eurymen* specimens, the ridge is still present, although the distance between arch 2 and 3 is increased. This ridge is absent in all other psychrolutids (state 1).

10. Arch 2 (A2) — This is a binary character. In *Ambophthalmos*, *Cottunculus*, *Dasycottus*, *Eurymen*, and *Malacocottus* specimens, arch 2 inserts laterally on the orbital ridge (state 0). In those of *Ebinania*,

Neophrynichthys, and *Psychrolutes* arch 2 inserts laterally well in from the orbit (state 1).

11. Arch 2 (A2) — This is a binary character. In specimens of *Ambophthalmos* arch 2 fuses medially to its antimere (state 1). In large *A. angustus*, arch 2 can be entirely fused medially, forming a continuous plate of bone from one orbital rim to the other. No other psychrolutids show a medial fusion of arch 2 (state 0); however, *Cottunculus* species have a similarly shaped arch 2, but it is medially separate from its antimere.

12. Arch 5 (A5) — This character is binary. In the primitive state, arch 5 is fused to the pterotic (state 0). In the derived state, arch 5 is separate from the pterotic and is tubular in form (state 1). The derived state is unique to all three *Psychrolutes* examined. In the derived state, this bone can be considered the anterior tabular of the pterotic.

13. Arch 6 (A6) — This character is binary. Arch 6 is either fused to the parietal (state 0) or is separate and tubular in form (state 1). The derived state is shared by *Ebinania*, *Malacocottus*, *Neophrynichthys*, and *Psychrolutes* spp.. Arch 6 may be homologous with the medial extrascapular seen in generalised percoids (Yabe, 1985).

14. Posterior tabular bone of the pterotic (anterior tabular of Nelson, 1982) — In the outgroups (and in all other cottoids Yabe, 1985, examined), this bone is fused to the pterotic (state 0). In all psychrolutids this bone is separate from the pterotic and tubular in form (state 1).

15. Posterior supratemporal (posterior tabular of Nelson, 1982) — Members of the outgroup, *Dasycottus*, and *Eurymen*, have this bone (state 0). All other psychrolutids lack this bone and have only one medial

supratemporal (medial tabular of Nelson, 1982) (state 1, Figure 5).

16. Medial supratemporal (medial tabular of Nelson, 1982) — This is a binary character. Typically, this bone is separate from the posterior tabular bone of the pterotic (state 0). In *Ambophthalmos* species, the medial supratemporal has its anterolateral edge fused with the posteromedial edge of the posterior tabular bone of the pterotic (state 1, Figure 5). *Cottunculus* species have these two tubular bones closely abutting in a similar manner to those of *Ambophthalmos*; however, they are two separate elements.

17. Medial supratemporal (medial tabular of Nelson, 1982) — This is a binary character. Typically the medial supratemporal is a discrete element (state 0). In *Ambophthalmos* specimens, the posterolateral edge connects to the anteromedial edge of the posttemporal via a narrow ridge (state 1, Figure 5).

18. Operculomandibular canal — This character is binary. Either this canal connects with the infraorbital canal or it does not (Figure 5). In all cottoid fish excluding psychrolutids, the two canals are separate (state 0). The connection of these two canals (state 1) is a diagnostic character of the Psychrolutidae (Yabe, 1985).

19. Infraorbitals 1, 2, and 3 (suborbitals) — This is a binary character. All specimens examined except those of *Cottunculus* lack spines on the infraorbital arches (state 0). *Cottunculus* fish have spines high on all arches of infraorbitals 1, 2, and 3 (state 1). *C. sadko* has poorly developed infraorbital spines, though small protuberances are still evident (Nelson, 1982).

20. Infraorbital 3 — This is a binary character. In the outgroups, the

arches on infraorbital 3 are extensive and openings for sensory pores are small. Psychrolutids have much larger spaces to allow passage of pores and the arches are narrow and high. In *Ambophthalmos*, *Cottunculus*, *Dasycottus*, and *Eurymen* specimens, the dorsal part of the arches on infraorbital 3 remain extensive and the two arches are dorsally fused (state 0, Figure 5). In specimens of *Malacocottus* and Psychrolutinae the two arches are well separated from each other (state 1).

21. Infraorbital (suborbital) stay — This is a binary character. Typically the infraorbital stay is evident as a posterior projection from the base of the third infraorbital (state 0). In *Psychrolutes paradoxus* and *P. sigalutes*, the infraorbital stay is elongate and very thin (state 1).

22. Infraorbitals 4, 5, and 6 (postorbitals) — This character has three unordered states. The outgroups have all three of infraorbitals 4-6 (state 0). Psychrolutids have lost one of these infraorbitals (state 1, Figure 5). It is likely that infraorbital 5 was lost since the last infraorbital articulates with the sphenotic and the fourth infraorbital articulates with the third in both the ingroup and outgroup. The connection point of the operculomandibular canal to the infraorbital canal (character 18, Figure 4) is approximately where infraorbital 5 is in the outgroups. These two state changes may be coincident. *Cottunculus* specimens have only one of infraorbitals 4-6 (state 2). It is probably homologous with infraorbital 6 of the outgroups, because it articulates with the sphenotic. Four infraorbitals (one postorbital) was a diagnostic character of *Cottunculus* (Nelson, 1982) until *Cottunculus nudus* Nelson, 1989, with five infraorbitals, was described.

23 & 24. Preopercular spines — Specimens of *Cottus*, *Jordania*,

Dasycottus, *Cottunculus*, and *Malacocottus* have preopercular spines. Two types of spines are observed: the first will be referred as primary spines, as these are typical of cottoids (Figure 6A and B). Primary spines are formed from projections off the posterior margin of the base of the preopercle and are directed posteriorly, in plane with the base of the preopercle. Members of all genera listed above, except *Cottunculus*, have primary spines. Primary spines are referred to as character 23, presence as state 0, and absence as state 1. Primary spines are likely homologous with the spines of the interior preopercular shelf described in larval red snapper (Pothoff, et al., 1988). In red snapper, these spines subdivide and reduce in size through ontogeny, forming a serrated posterior margin of the preopercle in adults.

Secondary spines form on the preopercular arches as projections of the anterior ridge of the preopercle (Figure 6B and C). They are usually perpendicular to the plane of the preopercle, but may angle anteriorly or posteriorly. Secondary spines are best developed in *Cottunculus* species, where every arch possesses a large secondary spine. Those of *Dasycottus* and *Malacocottus* have both primary and secondary spines. *Dasycottus setiger* has a small secondary spine on the anteriormost two arches. Those of *Malacocottus* have a very small secondary spine on the fourth and fifth arch (first being anteriormost). Secondary spines are referred to as character 24, absence as state 0, and presence as state 1. Secondary spines may be homologous with spines of the exterior preopercular shelf described in larval red snapper (Pothoff, et al., 1988). In red snapper, these spines subdivide several times in early ontogeny, but quickly disappear as the exterior shelf wraps around the preopercular canal. It is

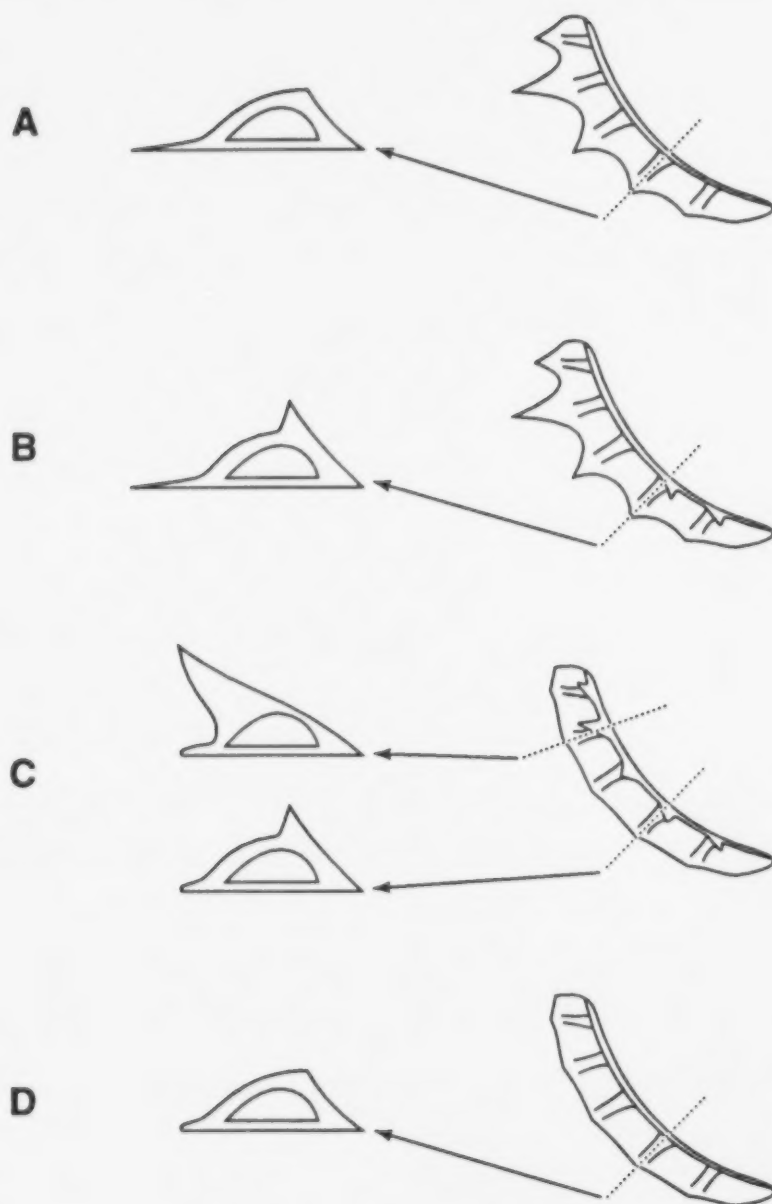


Figure 6. Primary and secondary preopercular spines. Left diagrams represent cross sections through preopercle on the right. A, primary spines as seen in *Cottus* and *Jordania*; B, primary and secondary spines as seen in *Dasycottus* and *Malacocottus*; C, secondary spines only, as seen in *Cottunculus*; D, absence of spines as seen in other psychrolutids.

likely that exterior shelf spines in psychrolutid larva wrap around the preopercular canal and fuse with the interior shelf (forming the base plate of the preopercle), forming the preopercular arches seen in adults. In this case, secondary spines would be neomorphic, possibly originating in a fashion similar to spines on the cranial and infraorbital arches. If so, spines borne on cranial canal arches would be a character complex unique to psychrolutids.

Pectoral and Pelvic Girdles

Psychrolutids have a specialized pectoral girdle (Figure 7). There is a trend in scorpaeniforms for a lengthening of the pectoral fin base and and pectoral girdle. Coincident with this, is a reduction in size of the coracoid (COR) and scapula (SC), and an increase in size of the actinosts (AC) (Yabe, 1985). Psychrolutids carry this trend to extremes. They typically have a very long pectoral fin base with between 19 and 26 long pectoral fin rays supporting a large fin. The coracoid and scapula are small and do not articulate with one another. There are always four large actinosts; the central two are the largest and articulate with the scapula or coracoid only slightly. Seven components make up the psychrolutid pectoral girdle (numbers in parentheses indicate number of elements): actinosts (4), cleithrum (CL), coracoid, postcleithra (0-2), posttemporal, scapula, and supratemporals (1-2). The posttemporal and supratemporals are discussed with the cranial canals and associated osteology.

The psychrolutid pelvic girdle is little specialized (Figure 8). In the typical cottoid, each basipterygium (BAS) is triangular to quadrangular and is medially sutured to its antimere along its length excepting a small

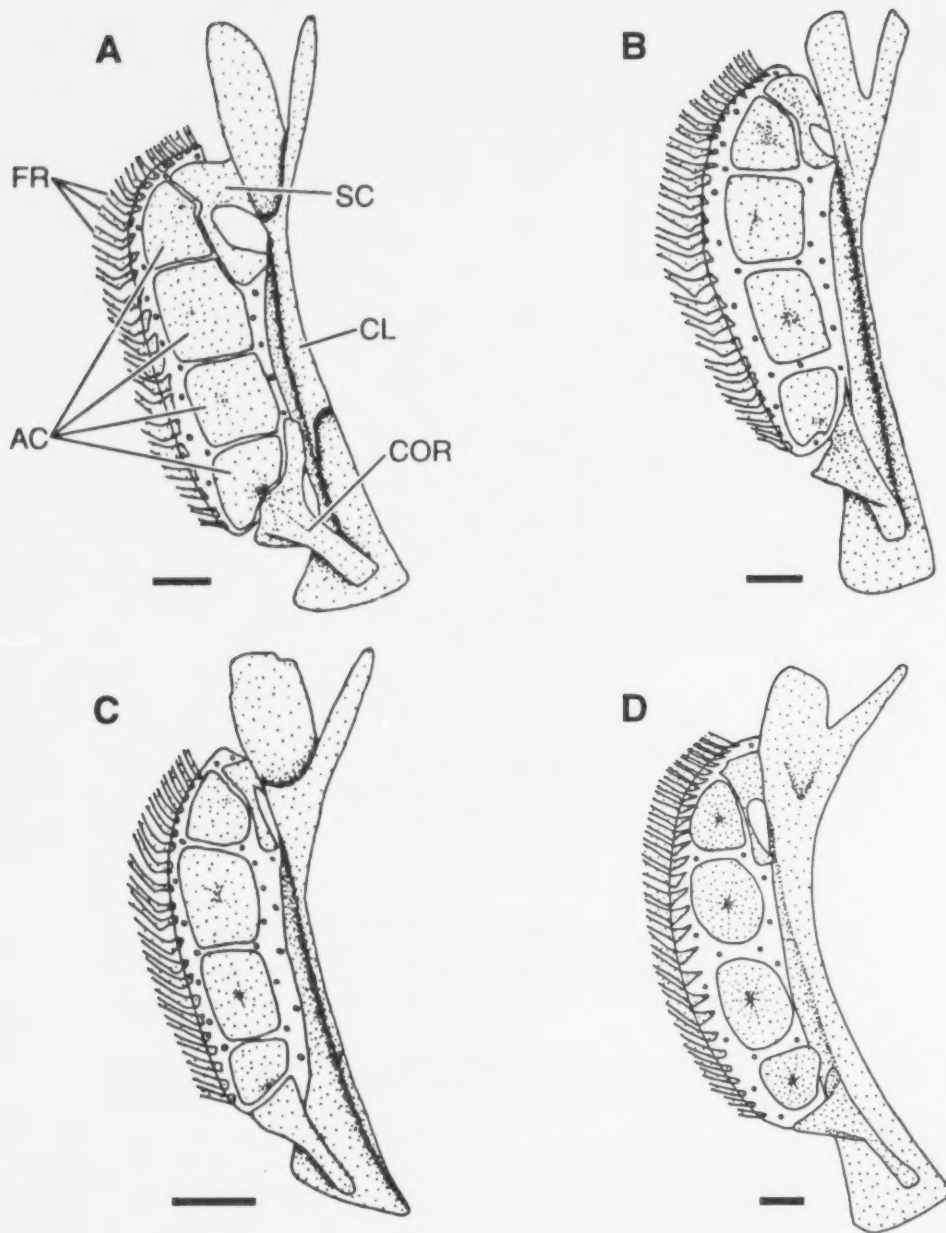


Figure 7. Pectoral skeleton in lateral aspect. A, *Dasycottus setiger*; B, *Neophrynichthys latus*; C, *Cottunculus thomsonii*; D, *Ambopthalmos angustus*. AC, actinost; CL, cleithrum; COR, coracoid; FR, fin ray; SC, scapula. Postcleithra, supracleithrum, and supratemporals not shown. Scale bars indicate 5 mm.

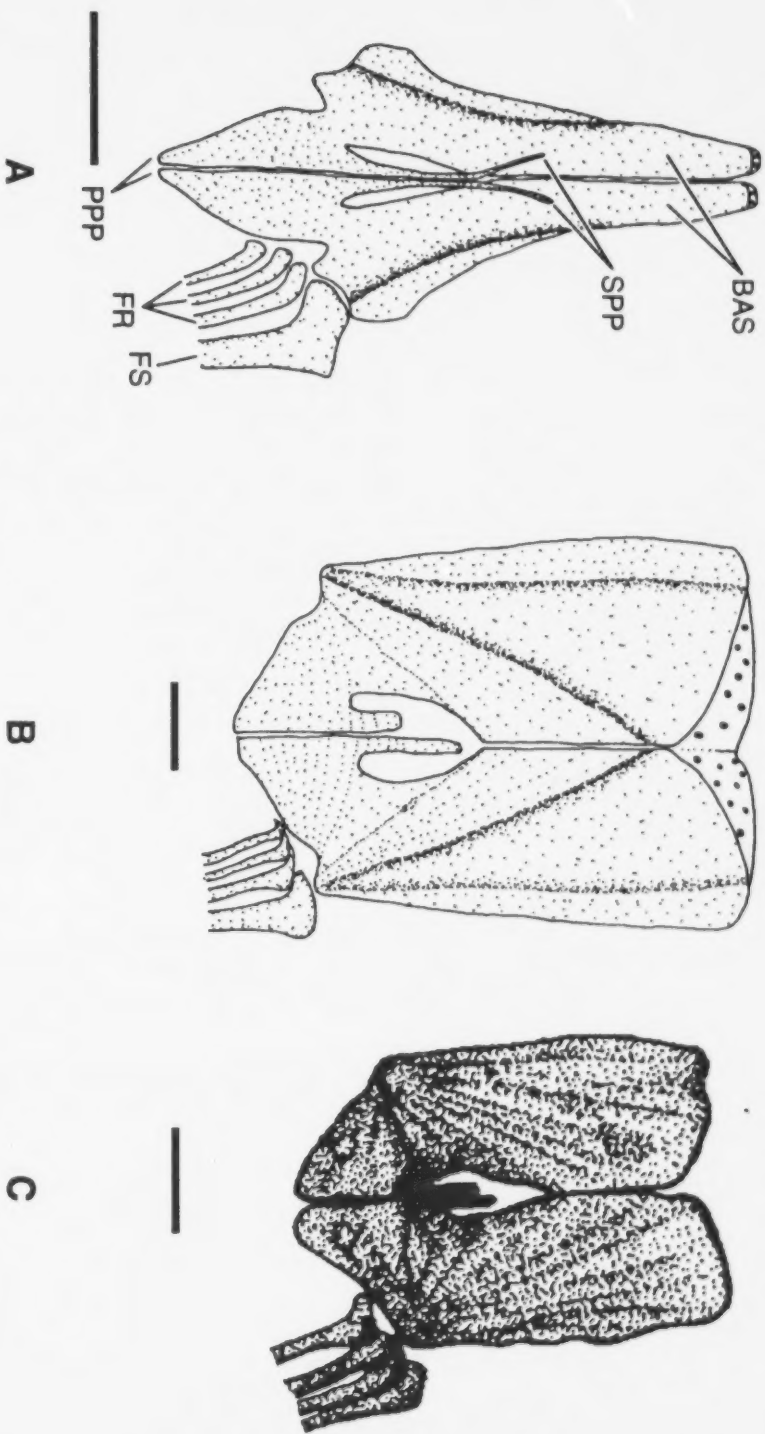


Figure 8. Pelvic girdle in ventral aspect. A, *Dasycoctus setiger*; B, *Ambloptilalmos angustus*; C, *Cottunculus granulatus*. BAS, basipterygium; FR, fin ray; FS, fin spine; PPP, postpelvic process; SPP, subpelvic process. Scale bars indicate 5 mm. (C, *Cottunculus granulatus*, after Nelson (1985)).

median gap. The posterior end of the basipterygia are extended to form the postpelvic process (PPP). Ventromedially, the subpelvic process (SPP) extends from each basipterygium into the median gap. Psychrolutids have a small pelvic fin supported by one spine and three rays.

25. Coracoid — This is a binary character. Typically, the coracoid extends dorsally along the anterior edge of the fourth (ventral most) actinost, sometimes reaching the third actinost (state 0, e.g., *Dasycottus setiger* and *Neophrynichthys latus*, Figure 7A and B). In *Ambophthalmos* and *Cottunculus* species, the coracoid is truncate, articulating only with the ventral edge of the fourth actinost (state 1, Figure 7C and D). The specimen of *A. angustus* diagrammed here (Figure 7D) has a small blunt dorsal projection on the coracoid; however, it is probably an abnormality since it does not exhibit the ossification grain typical of the rest of the coracoid and is not present in the other specimen examined. *Psychrolutes paradoxus* and *P. sigalutes* have a specialized dorsal extension of the coracoid, it being very long and narrow.

26. Coracoid-fourth actinost — This is a binary character. Typically, a posterior notch is present between the coracoid and fourth actinost (state 0, Figure 7A and B). This notch is greatest in *Psychrolutes paradoxus* and *P. sigalutes*, where the coracoid has only a small attachment to the fourth actinost. In *Ambophthalmos* and *Cottunculus* species, this notch is not apparent, and the coracoid completely articulates with the fourth actinost (state 1, Figure 7C and D).

27. Articulation of scapula and cleithrum — This is a binary character. In the outgroups and *Dasycottus* species, the scapula articulates with the cleithrum in two places, on either side of the scapular foramen (state 0,

Figure 7A). In all other psychrolutids the ventral articulation is lost and a cartilaginous gap is present (state 1, Figure 7B, C, and D). The scapular foramen allows passage of a branch of the ramus lateralis accessorius nerve.

28. Scapula-second actinost — This is a binary character. Typically the scapula articulates with the first and second actinosts (state 0, Figure 7A, C, and D). *Ebinania* and *Neophrynichthys* species have a reduced scapula, that only articulates with the first actinost (state 1, Figure 7B).

29. Actinost pores — This is a binary character. Actinost pores are unossified indentations between actinosts. Psychrolutids lack these indentations and have rectangular shaped actinosts (state 1). This is a diagnostic character of Psychrolutidae (Yabe, 1985). Other cottoids have anvil shaped actinosts creating pore-like spaces between the actinosts, actinost-scapula, or actinost-coracoid (state 0). In psychrolutids, a small notch is present between the first actinost and the scapula. This notch is not pore-like; however, it may be homologous to the pore observed in the same location in the outgroups.

30. Postcleithra — This is a multistate character with three unordered states. Typically two postcleithra are observed (state 0). In *Ambophthalmos* and *Cottunculus* specimens, one postcleithrum is observed (state 1). In *Psychrolutes paradoxus* and *P. sigalutes* postcleithra are absent (state 2). It is unlikely that the evolution of this character occurred in an ordered fashion since *P. paradoxus* and *P. sigalutes* have a reduced skeleton and probably lost both postcleithra in a single event, while *Ambophthalmos* and *Cottunculus* species have a well developed skeleton and a well ossified single postcleithrum.

31. Pelvic girdle — This is a binary character. In the outgroups, *Dasycottus*, and *Eurymen* specimens, the pelvic girdle progressively narrows out anteriorly to a blunt point (state 0, Figure 8A). In all other psychrolutids, the pelvic girdle expands anteriorly and has a concave anterior edge (state 1, Figure 8B and C). This dramatic change in form correlates with a change in depth of the V-shaped symphysis of the cleithra where the pelvic girdle articulates. In the primitive condition, the pectoral region of the fish is round to moderately compressed, resulting in a steep cleithral symphysis and a correspondingly narrow pelvic girdle to fit between the cleithra. In the derived state the pectoral region of the fish is more depressed, resulting in a shallower cleithral symphysis and an expanded pelvic girdle.

Caudal Skeleton

The psychrolutid caudal skeleton is little modified from the typical cottoid condition (Yabe, 1985). All cottoids have a well ossified caudal skeleton with the hypurals, parahypural, and urostyle fused, forming the plate-like hypural-parahypural complex bone (HC). Primitively, this complex bone is formed by two sutured plates (Figure 9A). The ventral plate is formed by the parahypural and hypurals 1 and 2 and the dorsal plate by hypurals 3-5 and the urostyle. In most cottoids and all psychrolutids these two plates are fused, at least anteriorly (Figure 9B-F). Usually three epurals (EPU) are present, although *Dasycottus setiger*, *Neophrynichthys latus*, and *Psychrolutes paradoxus* can have either two or three. The stegural element (STU) is present in some cottoids and in one psychrolutid, *Dasycottus setiger*. In psychrolutids, the caudal fin is

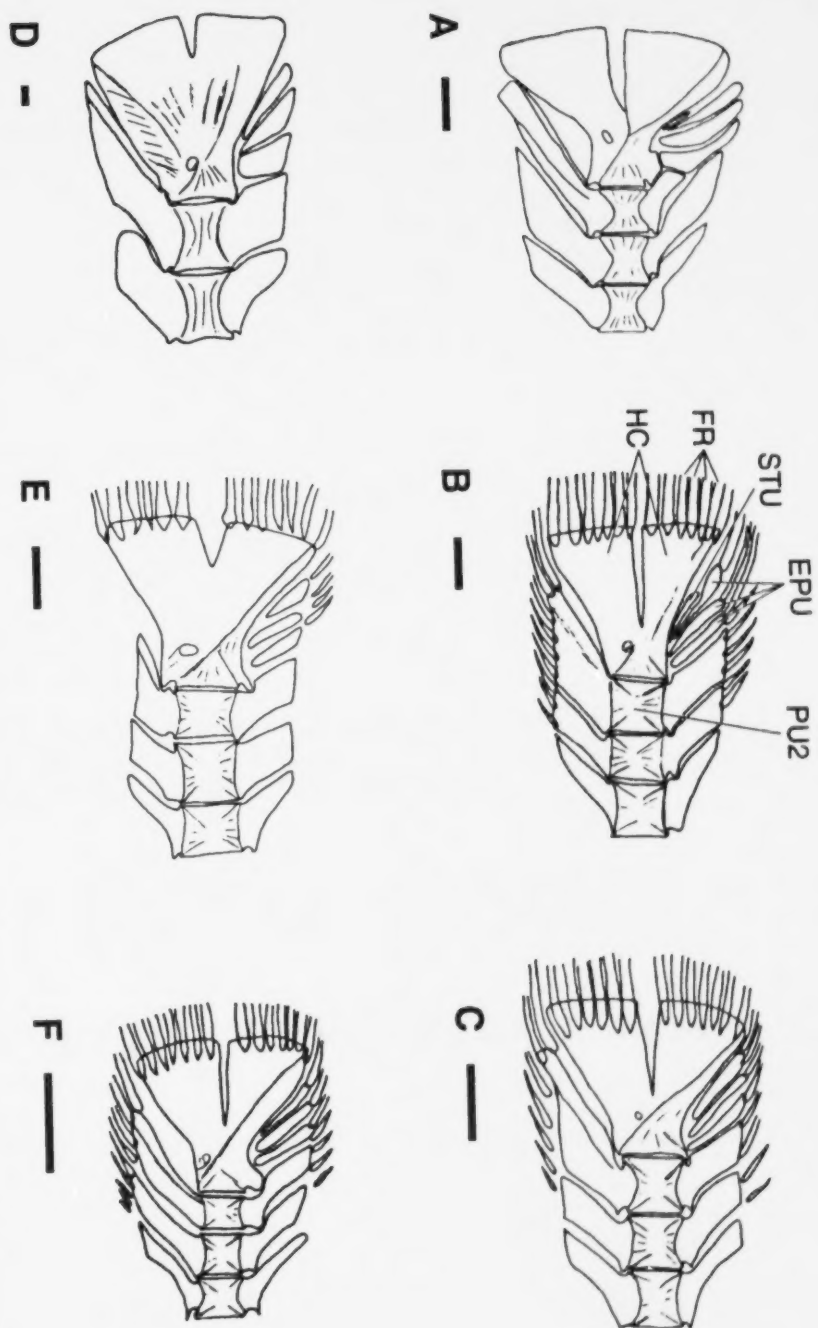


Figure 9. Caudal skeleton in lateral aspect. A, *Jordania zonope*; B, *Dasycoottus setiger*; C, *Malacocottus kincaidi*; D, *Cottunculus thomsonii*; E, *Ambloptalmos angustus*; F, *Psychrolutes paradoxus*. EPU, epural; FR, fin ray; HC, hypural-parahypural complex; PU2, preural centrum-2; STU, stegural. Scale bars indicate 1 mm.

composed of 11-14 principal rays attached to the hypural-parahypural complex and a series of procurrent rays dorsally attached to the epurals and the neural spine of preural centra-2 (PU2) and -3, and ventrally attached to the haemal spines of preural centra-2 and -3. Haemal spines are fused to preural centra-2 and -3 in all cottoids (Yabe, 1985).

32. Stegural element — This is a binary character. *Dasycottus setiger*, *Hexagrammus stelleri*, and *Jordania zonope* have the stegural element (state 0, Figure 9A and B). *Cottus ricei* and all psychrolutids other than *D. setiger* lack the stegural element (state 1, Figure 9C-F). Yabe (1985) reports the stegural in *Ebinania brephocephala*; however, none were present in the specimens I examined.

33. Hypural-parahypural plate fusion — This is a binary character. Typically, the dorsal and ventral plates of the hypural-parahypural complex bone are less than half fused (state 0, Figure 9A, B, C, and F).

In members of *Ambophthalmos* and *Cottunculus* the two plates are almost entirely fused, with only a small posterior notch (state 1, Figure 9D and E).

Soft Anatomy

34. Branchiostegal membranes — This is a binary character. In *Dasycottus*, *Hexagrammus*, and *Jordania* specimens, the branchiostegal membranes are medially fused and free from the isthmus (state 0). In *Cottus* species and in psychrolutids other than *Dasycottus*, the branchiostegal membranes are attached to a broad isthmus (state 1).

35. Cirri — This is a binary character. *Ambophthalmos*, *Dasycottus*, *Ebinania*, *Eurymen*, *Hexagrammus*, *Jordania*, *Malacocottus*,

Neophrynichthys species, and *Psychrolutes phrictus* have cirri present at least on their heads (state 0). *Cottus*, *Cottunculus*, *Psychrolutes paradoxus*, and *P. sigalutes* examined lack cirri (state 1). *Cottunculus nudus* is the only species in its genus known to have cirri (Nelson, 1989).

36. Skin prickles — This is a binary character. Typically skin prickles are present (state 0). *Ambophthalmos*, *Eurymen*, and the psychrolutine species examined lack skin prickles (state 1). *Dasycottus* species have a single row of skin prickles on either side of its dorsal fin, approximately half way between the lateral line and the dorsal fin. *Malacocottus* specimens have only the anterior most of these prickles, and they are embedded in the skin overlying the posttemporals. *Cottunculus* species have variously developed skin prickles, from very dense in *C. microps*, to almost absent in *C. nudus* (Nelson, 1989)

37. Hyohyoides inferioris — This is a binary character. Members of the outgroups, *Ambophthalmos*, *Cottunculus*, *Dasycottus*, *Eurymen*, and *Malacocottus* lack this muscle (state 0). Those of *Ebinania*, *Neophrynichthys*, and *Psychrolutes* have this muscle (state 1). The evolution of scorpaeniform hyoid musculature is discussed in Yabe (1985).

Phylogenetic Hypothesis

Character data were entered and edited in MacClade 3.04 (Maddison and Maddison, 1992) and analysed in PAUP 3.1.1 (Phylogenetic Analysis Using Parsimony, Swofford, 1993). All characters analysed were unweighted and unordered. The "branch and bound" search algorithm was used, as it finds all possible minimum length trees. Parsimony analysis of 37 informative characters resulted in three equally shortest trees. The ingroup is completely resolved and the three trees differ only in the arrangement of the outgroups. The strict consensus tree and character evolution as estimated by PAUP 3.1.1 is plotted in Figure 10. Tree statistics include: treelength=52, consistency index=0.75, homoplasy index=0.25, retention index=0.881, and rescaled consistency index=0.661.

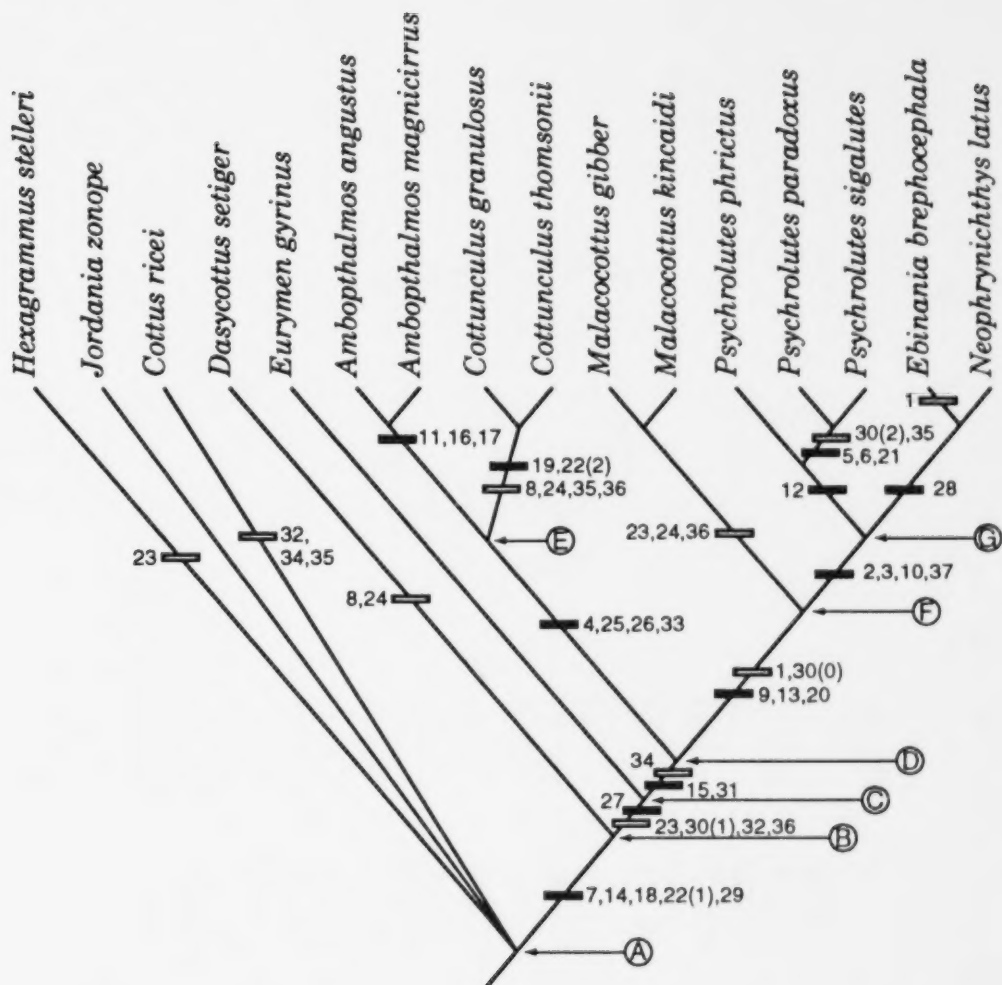


Figure 10. Cladogram of thirteen psychrolutid species estimated with 37 synapomorphic characters. Characters are indicated by number. Numbers in parentheses indicate state for multistate characters. Solid boxes indicate characters fully congruent with the tree. Open boxes indicate homoplastic characters. Circled letters point to nodes referred to in text.

Discussion

Character Evolution in Psychrolutidae

This section discusses cladogenesis and character evolution within Psychrolutidae as estimated by the phylogeny presented in Figure 10.

Psychrolutidae (clade B) is characterised by five synapomorphies. Reduction of bone covering sensory canals (7) and connection of the infraorbital and opercular sensory canals (18) are the most conspicuous characters diagnosing this family. Separation of the posterior tabular bone from the pterotic (14) and loss of actinost pores (29) also diagnose psychrolutids. Yabe (1985) examined sixty-one cottoids and did not encounter characters 7, 14, 18, or 29 outside the Psychrolutidae. Loss of one postorbital (22) is probably coincident with connection of the infraorbital and opercular sensory canals (18). Although character 18 is unique to Psychrolutidae within Cottoidea, loss of one postorbital (22) is not (Yabe, 1985).

Dasycottus setiger is sister to all other psychrolutids (clade C). One synapomorphic character and four homoplastic characters support the monophyly of clade C. Loss of the ventral articulation of the scapula to the cleithrum (27) occurred between node B and C. Loss of the stegural element (32) is homoplastic; clade C within Psychrolutidae and *Cottus ricei* lack this element. Loss of primary preopercular spines (23), one postcleithrum (30 (states 0 and 1)), and skin prickles (36) are plotted between nodes B and C by PAUP's character optimisation algorithm. These three characters (23, 30 (states 0 and 1), and 36) are homoplastic and may have a different evolution that will be discussed at the end of this section.

All psychrolutids excluding *Dasycottus setiger* and *Eurymen gyrinus* form a monophyletic group (clade D) supported by two synapomorphic characters and one homoplastic character. Loss of the posterior supratemporal (15), widening of the anterior part of the pelvic girdle (31), and fusion of the gill membranes to the isthmus (34) occurred between node C and D. The first two characters (15 and 31) are congruent with the tree, while the last character (34) is homoplastic in *Cottus ricei*.

Ambophthalmos and *Cottunculus* form a monophyletic group (clade E) supported by four synapomorphic characters. Inclusion of the sphenotic in the orbital rim (4), two characters of the coracoid (25 and 26), and advanced fusion of the hypural-parahypural (33) occurred between nodes D and E.

Three synapomorphic characters support the monophyly of *Ambophthalmos*. Medial fusion of arch 2 (11), fusion of the posterior tabular of the pterotic to the medial supratemporal (16), and fusion of the medial supratemporal to the posttemporal (17) are synapomorphic in *Ambophthalmos*.

Two synapomorphic and four homoplastic characters support the monophyly of *Cottunculus*. Spines on the arches of infraorbitals 1-3 (19) and only four infraorbitals (one postorbital, character 22(2)) are synapomorphies of *Cottunculus*. Spines on cranial arches (8), secondary preopercular spines (24), absence of cirri (35), and presence of skin prickles (36) are homoplastic characters supporting the monophyly of *Cottunculus*. The evolution of characters 8 and 24 may be different from that plotted by PAUP, and is discussed at the at the end of this section.

Psychrolutinae (*Ebinania*, *Neophrynichthys*, and *Psychrolutes*) and

Malacocottus form a monophyletic group (clade F) supported by three synapomorphic and two homoplastic characters. Separation of arches 2-3 from each other (9), separation of arch 6 from the parietal (13), and separation of the arches on infraorbital 3 (20) are synapomorphic in this group. Teeth on the vomer (1) and two postcleithra (30(0)) are homoplastic character transformations between nodes D and F. Teeth on the vomer (1) is lost in this clade and regained in *Ebinania*. Character 30(0) is a reversion from the derived state of having one postcleithra to the primitive condition of two postcleithra. The evolution of character 30 will be discussed at the end of this section.

Sister to *Malacocottus* is Psychrolutinae (clade G), a monophyletic group supported by four synapomorphies. Reduced ossification of the skull (2), laterally projecting frontals (3), arch 2 far from orbital rim (10), and presence of the hyohyoides inferioris muscle (37) are synapomorphic in this group.

The monophyly of *Psychrolutes* is supported by one synapomorphic character. Separation of Arch 5 from the pterotic (12) is shared by all *Psychrolutes* examined. *P. paradoxus* and *P. sigalutes* are a monophyletic group supported by three synapomorphies and two homoplastic characters. Protruding autosphenotic (5), specialized rod-like subopercle (6), and narrow elongate infraorbital stay (21) are synapomorphic in these two species. Loss of both postcleithra (30(2)) is unique to these two species. Loss of skin cirri is shared between *P. paradoxus* and *P. sigalutes*, and is homoplastic in *Cottunculus*.

Ebinania and *Neophrynichthys* form a monophyletic group based on one synapomorphic character. They both share a reduced scapula that

articulates with only the first actinost (28).

Of the thirty-seven characters examined, twenty-eight are fully congruent with the tree and nine are homoplastic. Two characters, 32 and 34, are homoplastic between the ingroup and one of the outgroups (each has a CI(consistency index)=0.5). Two characters, 23 and 35, are homoplastic between the outgroups and two nodes in the ingroup (each has a CI=0.333). Three characters, 1, 8, and 30, are homoplastic between two nodes in the ingroup (1 and 8 have a CI=0.5, 30 is a multistate character with only one state being homoplastic, it has a CI=0.666). Two characters, 24 and 36, are homoplastic between three nodes in the ingroup (each has a CI=0.333). Evolution of characters 1, 8, 24, 32, 34, and 35 is resolved on the tree. Characters 23, 30(states 0 and 1), and 36 are not fully resolved and evolution of these characters is equivocal between certain nodes of the tree.

Characters 8, 23, 24, 30 (states 0 and 1), and 36 may have a different evolution from what was estimated by PAUP's character optimisation algorithm. Here, I discuss alternative hypotheses to the evolution of these characters (Figure 11).

The most parsimonious evolution of spines borne on cranial arches (8) involves two steps, evolving independently in *Cottunculus* and *Dasycottus*. If cranial arch spines were a primitive character for all psychrolutids, four evolutionary steps, one gain and three independent losses, resulted in the pattern observed today. The gain would be in an ancestral psychrolutid (nodes A to B). The lineages leading to *Ambophthalmos*, *Eurymen*, and the monophyletic group composed of *Malacocottus* and Psychrolutinae (clade F) would have independently lost

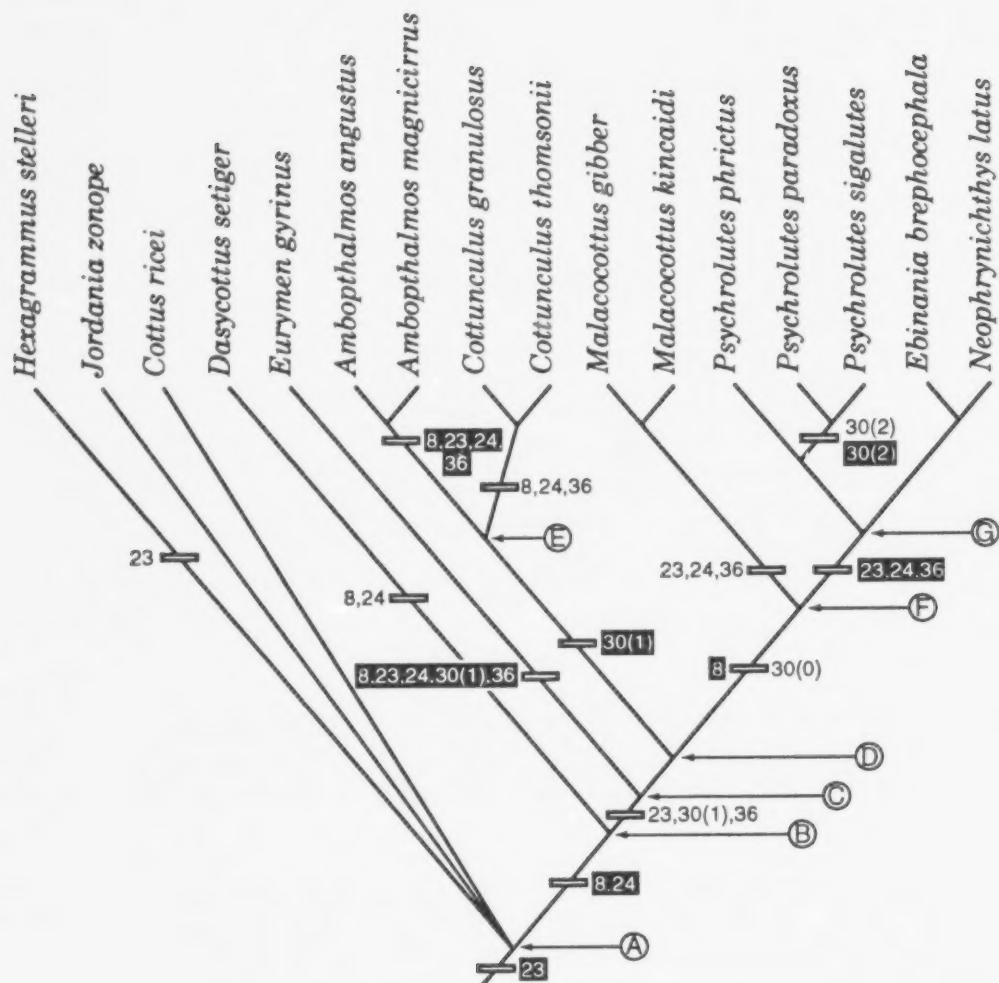


Figure 11. Evolution of characters 8, 23, 24, 30, and 36. Characters in normal type were plotted by PAUP optimisation algorithm. Characters plotted in reverse type show alternative hypotheses of character evolution described in text. Circled letters point to nodes referred to in text.

their cranial spines.

The most parsimonious evolution of secondary preopercular spines (24) involves three steps, the lineages *Cottunculus*, *Dasycottus*, and *Malacocottus* independently acquiring this character. If the presence of secondary preopercular spines is primitive for psychrolutids, its evolution would require four steps. The first would be acquisition of this character in a psychrolutid ancestor (node A to B), and then three independent losses occurring in *Ambophthalmos*, *Eurymen*, and clade G.

Spines borne on cranial, infraorbital, and preopercular arches may be a character complex unique to psychrolutids. If this is the case, loss of spines on various arches (*e.g.*, characters 8, 19, and 24) would be the derived condition. An ontogenetic series would prove invaluable in determining the polarity of such characters.

The evolution of primary preopercular spines (23) is not resolved between nodes A and B. Presence of primary preopercular spines is most likely the primitive condition of psychrolutids, other cottoids, and hexagrammids because primary spines are ubiquitous among scorpaeniforms, including hexagrammids other than *Hexagrammus*. The loss of these primary preopercular spines in *Hexagrammus* is a derived condition (Shinohara, 1994). The most parsimonious evolution of primary spines within Psychrolutidae (clade B) involves two steps, its loss in clade C, and independent gain in *Malacocottus*. If the spines seen in *Malacocottus* are primitive, three lineages (*Eurymen*, clade E, and clade G) would have independently lost these spines. This would involve three steps opposed to two steps of the most parsimonious evolution of primary preopercular spines in psychrolutids.

The evolution of the postcleithra (30 (states 0 and 1)) probably did not occur as plotted by PAUP, in which one postcleithral element is lost between nodes B and C and regained between nodes D and F. It is equally parsimonious and more likely that one postcleithral element was lost independently in *Eurymen* and in the lineage leading to *Ambophthalmos* and *Cottunculus* (nodes D to E).

The evolution of skin prickles (36) involves three steps. The first step is a loss between nodes B and C, and reacquisition in the lineages leading to *Cottunculus* and *Malacocottus*. An equally parsimonious and more probable evolution of skin prickles involves three independent losses, in *Ambophthalmos*, *Eurymen*, and clade G.

Systematic Treatment

In this section a cladistic classification of Psychrolutidae is presented in which *Ambophthalmos* gen. nov. is established. This classification reflects psychrolutid interrelationships to the generic level. Three new subfamilies are established, Cottunculinae is redefined, and Psychrolutinae is maintained.

Nelson (1982) divided Psychrolutidae into two subfamilies, Cottunculinae and Psychrolutinae. The phylogeny I have reconstructed (Figure 12) does not support this classification. Psychrolutinae, as per Nelson (1982), is a monophyletic group. However, Cottunculinae, as per Nelson (1982), is paraphyletic. I maintain Psychrolutinae, redefine Cottunculinae to be a monophyletic taxon, and establish three new subfamilies, Dasycottinae, Eurymeninae, and Malacocottinae. These five subfamilies are diagnosed and sequenced below (Figure 12). Characters autapomorphic for each group are listed first, followed by homoplastic character combinations used in diagnosing each clade.

Family Psychrolutidae

Diagnosis

Synapomorphic diagnostic characters include: four well developed cranial arches on each frontal, rimming the orbit; one arch on pterotic (separate tubular bone in *Psychrolutes* examined); one arch on parietal (separate tubular bone in *Ebinania*, *Malacocottus*, *Neophrynichthys*, and *Psychrolutes*); posterior tabular of the pterotic is separate and tubular; opercular canal connected to infraorbital canal between last and second last infraorbital; pores between actinosts absent.

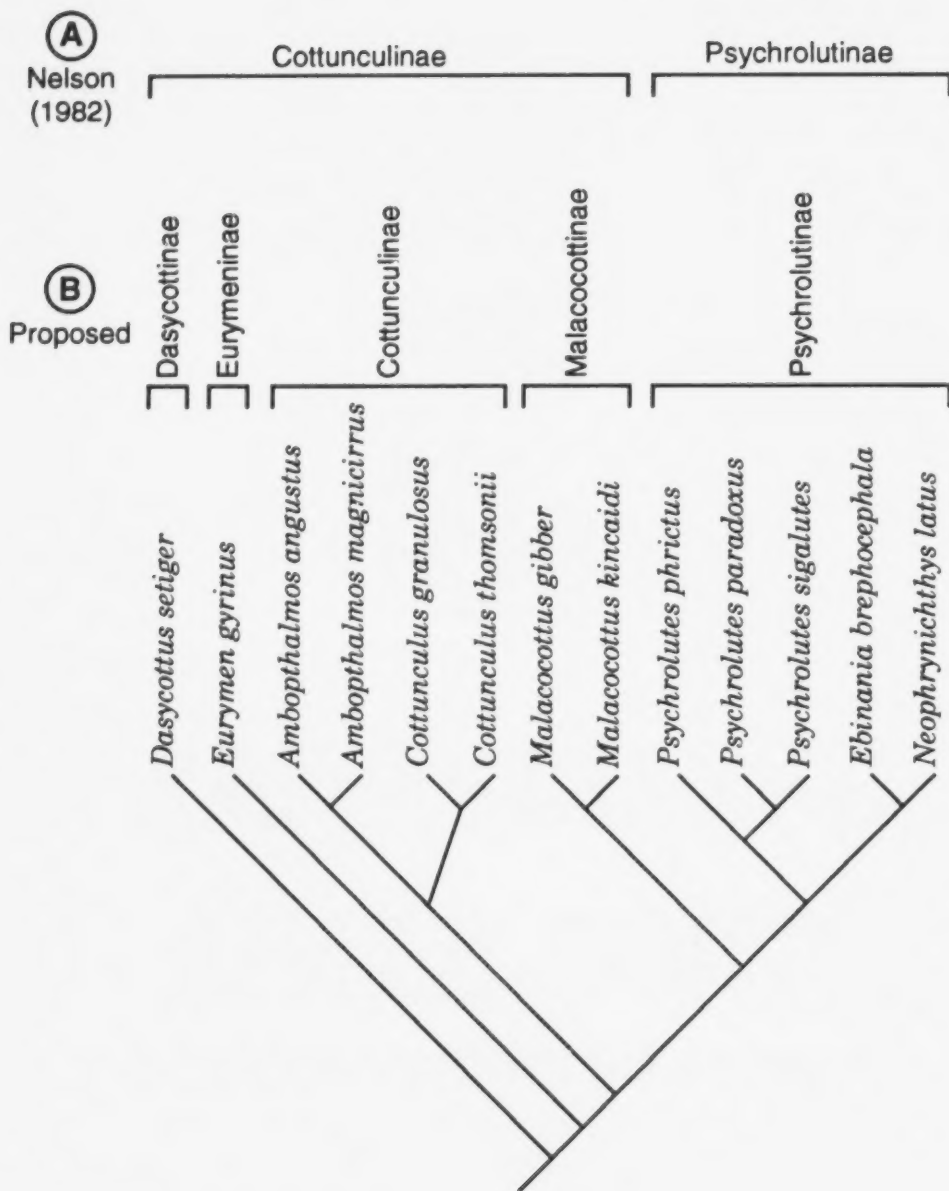


Figure 12. Comparison of proposed cladistic classification (B) to Nelson's (1982) synthetic classification (A) of Psychrolutidae. The cladistic classification sequence is: Dasycottinae, Eurymeninae, Cottunculinae, Malacocottinae, and Psychrolutinae. Psychrolutinae does not include Malacocottinae for reasons given in text.

Subfamily Dasycottinae

Includes: Dasycottus setiger Bean, 1890

Diagnosis

Homoplastic character combinations diagnostic of Dasycottinae include: well developed primary preopercular spines; well developed spines on cranial arches; two supratemporals present; rigid interorbital region; gill membranes fused and attached to isthmus anteriorly (all other psychrolutids have gill membranes fused to isthmus).

Differs from *Cottunculus* in having primary preopercular spines, two supratemporals, and no spines on infraorbitals. Differs from all other psychrolutids in having spines borne high on cranial arches.

Comments

Dasycottus setiger is the most generalised cottoid-like psychrolutid and shows few specialized characters. Spines borne on cranial arches may be a specialization of this genus or a primitive psychrolutid condition. If the latter is true, these spines would be homologous to those observed in *Cottunculus*. This character is described in the phylogenetic hypothesis section (on page 46).

Subfamily Eurymeninae

Includes: Eurymen gyrinus Gilbert and Burke, 1912

Diagnosis

Homoplastic character combinations diagnostic of Eurymeninae include: no spines on cranial, infraorbital, and preopercular arches; rigid interorbital region; two or three supratemporals (one posterior and one or two medial); vomerine teeth.

Differs from *Ambophthalmos* in having vomerine teeth and more than one supratemporal. Differs from *Cottunculus*, Dasycottinae, and Malacocottinae in not having primary or secondary preopercular spines. Differs from Psychrolutinae in having a rigid interorbital region.

Comments

Eurymen gyrinus is a specialized basal psychrolutid. *E. gyrinus* shows convergence with Psychrolutinae in having puffy skin, a broad depressed head, and a loosely articulated suspensorium. However, primitive features, such as presence of the posterior supratemporal, arch 6 fused to the parietal, and primitive pectoral and pelvic girdles, point to a more basal split in psychrolutid evolution.

Subfamily Cottunculinae

Includes: Ambophthalmos gen. nov.

Cottunculus Collett, 1875

Diagnosis

Synapomorphic diagnostic characters include: sphenotic contributing to orbital ridge; specialized coracoid (characters 25 and 26). Homoplastic character combinations diagnostic of Cottunculinae include: no primary preopercular spines; rigid interorbital region; one supratemporal; arch 6 fused to cranium. Although less definitive than synapomorphies, the last four characters are readily observable and practical.

Differs from Dasycottinae and Eurymeninae in having no more than one supratemporal. Differs from Malacocottinae in having arch 6 fused to the parietal and lacking primary preopercular spines. Differs

from Psychrolutinae in having a rigid interorbital region and arch 6 fused to the parietal.

Genus *Ambophthalmos* gen. nov.

Includes: Ambophthalmos angustus (Nelson, 1977)

Ambophthalmos magnicirrus (Nelson, 1977)

Type designation

Nelson (1977) described *Neophrynichthys angustus* and *N. magnicirrus*. I place both species in the new genus, *Ambophthalmos*. I designate *Ambophthalmos angustus* as the type of the genus since it is the first species described in Nelson (1977). In addition, *A. angustus* was the first species collected (in 1962 vs. 1967).

Diagnosis

Synapomorphic diagnostic characters include: posterior tabular of the pterotic fused to medial supratemporal; medial supratemporal fused to posttemporal by thin ridge; medial fusion of A2 to its antimere. Homoplastic character combinations diagnostic of *Ambophthalmos* include: cranial and infraorbital arches lack spines; rigid interorbital region; absence of primary and secondary preopercular spines; one supratemporal; no vomerine teeth.

Differs from *Cottunculus* and Dasycottinae in lacking spines on cranial arches and lacking vomerine teeth. Differs from Malacocottinae in lacking preopercular spines. Differs from Eurymeninae in having only one supratemporal and lacking vomerine teeth. Differs from Psychrolutinae in having a rigid interorbital region and cranial arch 6 fused to the parietal.

Description

Body generally tadpole shaped. Head large, trunk short and tapering to a small tail. Head round to slightly depressed at orbits, moderately depressed (approximately 1.5 times as wide than high) at opercles, body round to slightly depressed at pectoral bases, compressed at caudal penduncle. Orbits rimmed by conspicuous ridges making the interorbital region concave in some specimens (especially juveniles). Mouth large, terminal, low, and slightly oblique. Lower jaws sometimes slightly protruding. Vomer toothless. Premaxilla with $2\frac{1}{2}$ -6 irregular rows of teeth, dentary with $2\frac{1}{2}$ -6 irregular rows of teeth. Cirri on head well developed in both species: cirri large and frilled in *A. magnicirrus*, cirri smaller and usually undivided in *A. angustus*. Cirri concentrated and largest on mandible, dorsal rim of orbit, and rostrum. Between 11-12 widely spaced lateral line pores, with first just posterior to supracleithrum and last medially on the caudal penduncle. The lateral line starts high on the body but sweeps to a medial position at about the fifth pore.

Dorsal fin with deep notch between spinous and soft-rayed parts. Caudal fin slightly rounded to square. Fin meristics and measurements given in detail in Nelson (1977).

Ground colour in alcohol light tan. Chestnut brown markings in *A. angustus*; reddish brown markings in *A. magnicirrus*. Ventral surface light and unmarked in both. In young *A. angustus* and adult *A. magnicirrus*, markings tend to be irregular blotches with several large ones around the eye, and two large concentrations around the spinous

and soft dorsal fins (on the body and fin base). Young *A. angustus* tend to have more small blotches interspersed between the large patches than *A. magnicirrus*. In adult *A. angustus*, these blotches break up into a multitude of small spots, typically in the configuration of one large spot surrounded by a circle of smaller spots (see colour face plate). *A. magnicirrus* also shows this configuration of a large spot surrounded by a ring of small spots; but this pattern is faint and best represented on the pectoral fins. Peritoneum with dark flecks; moreso in *A. angustus* than *A. magnicirrus*.

Distribution

Ambophthalmos angustus has been collected and positively identified from: New Zealand coastal waters; Chatham Rise (east of South Island at 44°S); Bounty Platform (48°S, 180°W); Campbell Rise (52°S, 170°W); Auckland Island Shelf (50°S, 167°W). Presumed records of *A. angustus* collected by the Japanese Trawler "R. V. Kaiyo Maru" (Nelson, 1977) include: Pukaki Rise (49°S, 173°E); Antipodes Islands (50°S, 179°W approximately).

Ambophthalmos magnicirrus is known only from the Northeast coast of Macquarie Island (54°S, 159°E). More northerly populations may exist as the Macquarie Ridge extends to New Zealand.

Etymology

The name *Ambophthalmos* is derived from the Greek adjective, *ambon* (m.) and noun, *ophthalmos* (m.). The former refers to the ridge bordering the latter, eye (Brown, 1956). Together, this name describes the protruding orbital ridges characteristic of *A. angustus* and *A. magnicirrus*.

Genus *Cottunculus* Collett, 1875

Includes: *Cottunculus granulosus*, Karrer, 1968
Cottunculus microps, Collette, 1875
Cottunculus nudus, Nelson, 1989
Cottunculus sadko, Essipov, 1937
Cottunculus thomsonii, (Günther, 1882)

Diagnosis

Synapomorphic diagnostic characters include:, spines present on infraorbital arches (small protuberances to tall spines); secondary spines on preopercular arches are very well developed (compared with the minute spines of Dasycottinae and Malacocottinae). Homoplastic character combinations diagnostic of *Cottunculus* include: spines present on cranial arches; one supratemporal; no primary preopercular spines; rigid interorbital region.

Differs from *Ambophthalmos* and all other Psychrolutids in having spines on cranial, infraorbital, and preopercular arches. Differs from *Dasycottus* in having spines or protuberances on infraorbital arches, well developed secondary preopercular spines, and one supratemporal.

Subfamily Malacocottinae

Includes: *Malacocottus gibber* Sakamoto, 1930
Malacocottus kincaidi Gilbert and Thompson, 1905

Diagnosis

Homoplastic character combinations diagnostic of Malacocottinae include: no spines on cranial arches; primary preopercular spines; one supratemporal; Arch 6 is tubular and separate from the parietal; interorbital region rigid.

Differs from *Ambophthalmos*, *Eurymeninae*, and *Psychrolutinae* in having primary preopercular spines. Differs from *Cottunculus* and *Dasycottinae* in lacking vomerine teeth and cranial arch spines.

Subfamily Psychrolutinae

Includes: Psychrolutes Günther, 1861

Ebinania Sakamoto, 1932

Neophrynichthys (Hutton, 1875)

Diagnosis

Synapomorphic diagnostic characters include: orbital ridge thin and extending over eye, increasing interorbital space; skull roof soft, especially the frontals; hyohyoides muscle present. Homoplastic character combinations diagnostic of *Psychrolutinae* include: arch 6 is tubular and separate from the parietal; primary preopercular spines not present.

Differs from other four subfamilies in having a soft interaorbital region and specialised thin orbital ridge.

Comments

The sequencing of these three genera is provisional as only one character, scapula articulating with only first actinost (28), supports this sequence. *Psychrolutinae* are a diverse group of seventeen species. Further work, beyond the scope of this project, is required to improve our understanding of psychrolutine interrelationships.

A cladistic classification would be maintained by placing *Malacocottus* in *Psychrolutinae*; however, I maintain *Psychrolutinae* as per Nelson (1982), because *Ebinania*, *Neophrynichthys*, and *Psychrolutes* are a well defined group (Nelson, 1982). In addition, the inclusion of *Malacocottus* may prove unstable with future systematic work.

Biogeographic History of Cottunculinae
(Ambophthalmos and Cottunculus)

Psychrolutidae probably originated in the northern Pacific (Figure 13A). The two earliest lineages in the family (*Dasycottus* and *Eurymen*) are found along the Asian and North American Pacific Coasts. *Ebinania*, *Malacocottus*, and *Psychrolutes* are also represented in this region. The New Zealand region (including Macquarie Island) (Figure 13B) also holds a diversity of psychrolutids, with one or more species of *Ambophthalmos*, *Cottunculus*, *Ebinania*, *Neophrynichthys*, and *Psychrolutes* being represented. Southern South American waters (Figure 3 and 13C) have three species in three genera represented: *Cottunculus*, *Neophrynichthys*, and *Psychrolutes*. North Atlantic waters (Figure 13D) have only one species of *Ebinania* and one of *Psychrolutes*; however, three of *Cottunculus* are present. Several species of *Psychrolutes* are scattered around African and Australian waters (Figure 3). References relevant to psychrolutid distribution include: Federov and Nelson (1986), Fricke (1990), Nelson (1977), Nelson (1982), Nelson (1989), Nelson and Nakamura (1980), Nelson *et al.* (1985), Suzuki and Kimura (1980), and Yabe *et al.* (1983).

Cottunculinae may have originated in the north Pacific; however, no extant (or fossilised) species are present in this region. It is more likely that a pre-cottunculine arrived in the New Zealand region via an equatorial crossing from the north Pacific (Figure 13A-B). The New Zealand region is likely the centre of origin for Cottunculinae. There, two lineages diverged in this subfamily, *Ambophthalmos* and *Cottunculus*. Possibly Macquarie Island provided the allopatry necessary for this split.

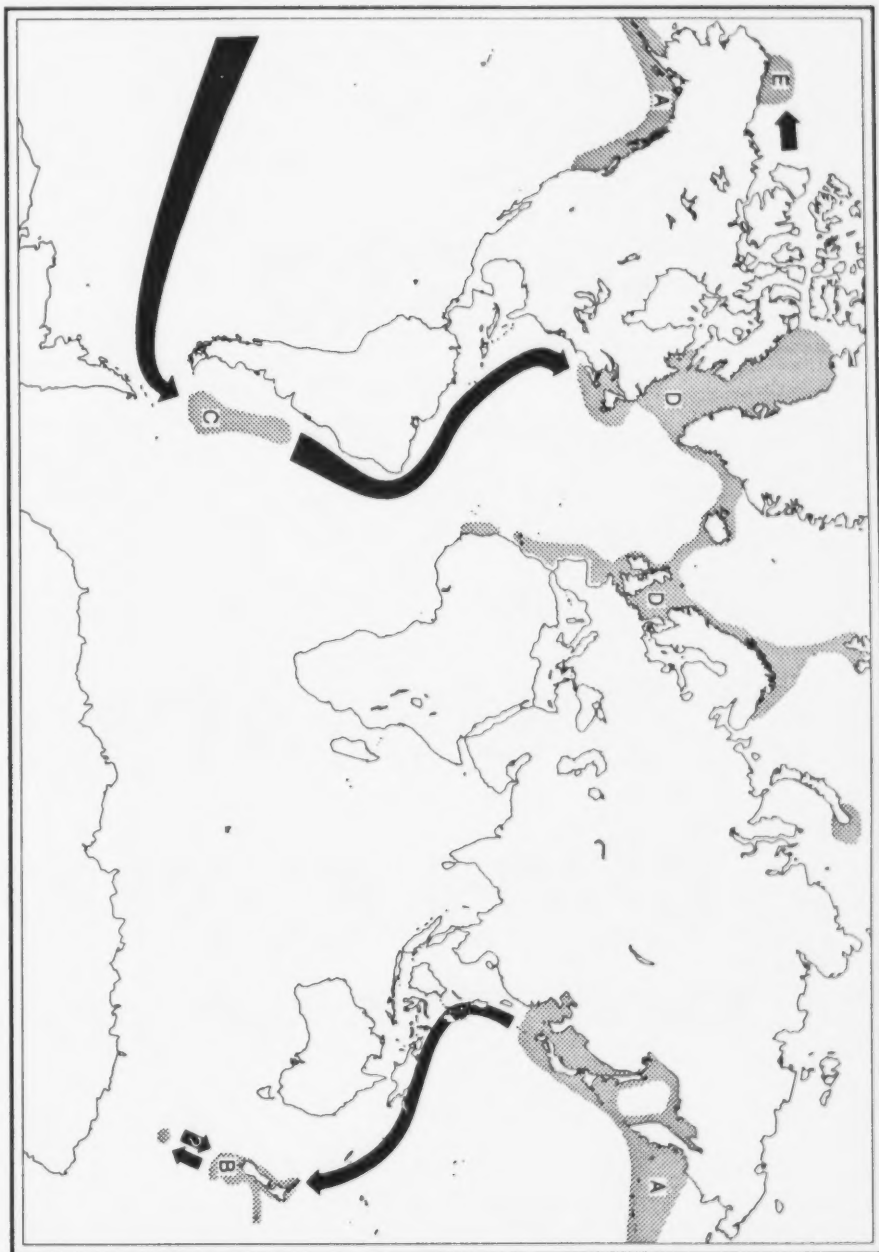


Figure 13. Biogeographic history of Cottunculinae (*Ambophthalmos* and *Cottunculus*). A, centre of psychrolutid origin; B, centre of cottunculine origin; C, *C. granulosus*; D, maximum diversity of *Cottunculus* (3 species); E, isolated *C. sadko* population. Arrows indicate routes of dispersal.

If this were the case, *Ambophthalmos* originated around Macquarie Island while *Cottunculus* originated around New Zealand. A pre-*A. angustus* would have invaded New Zealand after this split. *Cottunculus nudus*, the only member of its genus found in New Zealand Waters, is probably sister to all other *Cottunculus* species because it possesses several characters primitive for that genus (e.g., small cirri are present, skin prickles are very sparse to absent, two postorbitals are present). This is evidence for New Zealand being the centre of origin for *Cottunculus*.

The next dispersal event for *Cottunculus* was from New Zealand to South America (Figure 13B-C). *Cottunculus granulatus* is the only species of its genus present in this region. This species has one postorbital, skin prickles, and lacks cirri, all advanced characters of the genus. Its morphology is similar to *C. nudus* of New Zealand and *C. thomsonii* of the North Atlantic (Nelson and Nakamura, 1980).

The next dispersal event for *Cottunculus* was an equatorial crossing to the north Atlantic via the western Atlantic (Figure 13C-D). A somewhat continuous distribution exists today, from North American to European waters via Greenland and Iceland. Perhaps this large and not entirely continuous region provided the allopatric conditions necessary for diversification of *Cottunculus* into the three species seen there today, *C. microps*, *C. sadko*, and *C. thomsonii*. The last dispersal event for *Cottunculus* was along the Canadian Arctic to the Beaufort Sea off Alaska where an isolated population of *C. sadko* is found (Figure 13D-E).

An alternative hypothesis of the biogeographic history of Cottunculinae would be almost opposite to the one described above. In this case, the cottunculine ancestor crossed the Canadian Arctic to the

Atlantic, then to South America, and then to New Zealand where *Ambophthalmos* is a recent *Cottunculus* derivative. This hypothesis is less likely as several morphological characters would require additional steps of evolution. For example, the postorbital and cirri would be lost in the cottunculine ancestor, and regained in *C. nudus* and *Ambophthalmos*. The first hypothesis is more plausible.

Present day cottunculine distribution is probably a result of dispersal. Vicariant events are not likely responsible for the disjunct distribution of Cottunculinae observed today. Past geography, however, may have provided routes of dispersal other than those shown in Figure 13.

If the pre-cottunculine ancestor arrived in New Zealand before formation of the Antarctic convergence (late Eocene), it may have dispersed via South America and Australia rather than via islands of the west Pacific as indicated in Figure 13A-B. If this were the case, cottunculine-like psychrolutids would be expected in Australian waters; but none are known from there today. It is more likely that the pre-cottunculine arrived in New Zealand via the west Pacific after the Eocene and then dispersed to South America (as indicated in Figure 13A-B-C). Finding cottunculines around central-south Pacific islands (e.g., Easter Island) would be strong support for this hypothesis.

Cottunculine dispersal from the south to north Atlantic likely occurred along the coasts of South and North America (Figure 13C-D). This equatorial crossing probably occurred after the connection of the Americas (late Pliocene) as no north Pacific cottunculines are known. This would date the speciation of the three north Atlantic species of *Cottunculus* within the last three million years.

Conclusions

Determining the relationships of *Ambophthalmos* provides insight into the evolution of Psychrolutidae. Nelson (1982) hypothesised that Psychrolutidae is composed of two monophyletic groups. Anatomical homologues studied here suggest that psychrolutid phylogeny is a series of nested monophyletic groups. *Ambophthalmos* is closest to *Cottunculus* and these two genera are closest to a clade made up by *Malacocottus* and Psychrolutinae. *Dasycottus* and *Eurymen* are earlier lineages off the main psychrolutid stem.

The two major clades in the family are Cottunculinae (7 species) and Psychrolutinae (17 species). Cottunculinae are prominent in the North Atlantic, Psychrolutinae in the Pacific and around South Africa, and both are represented in New Zealand waters. The other three lineages, Dasycottinae, Eurymeninae, and Malacocottinae are not diverse and are restricted to the north Pacific. The New Zealand region is hypothesised to be the centre of origin of Cottunculinae.

Since the original species descriptions (most of which were before 1940), few papers dealing with psychrolutid systematics have been published, and most of these by a single author (Nelson). This study provides the most comprehensive osteological study and phylogenetic interpretation of Psychrolutidae, and the first cladistic classification of this family. The classification presented here should provide a stable framework as new species (and genera) are described and phylogenetic relationships are better resolved. This is especially desirable for this family as new species will likely be found as remote areas and deep waters are better sampled.

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Appendix I

Summary of Character Descriptions

<u>Character</u>	<u>States</u>
1 vomer	0: toothed 1: teeth absent
2 skull roof	0: well ossified 1: poorly ossified and flexible
3 orbital ridge	0: normal 1: thin and forms an exaggerated dorsal wall of the orbit
4 sphenotic	0: not included in orbital rim 1: included in orbital rim
5 sphenotic groove	0: normal 1: borne on lateral process of sphenotic
6 subopercle	0: blade like "normal cottid-like" 1: thin and rod like
7 cranial sensory canals	0: covered extensively by bone 1: bone covering reduced to arches
8 spines on cranial arches	0: absent 1: present
9 arch 2-3 (A2-A3)	0: fused laterally 1: separate from each other
10 arch 2 (A2)	0: originates on orbital ridge 1: far from orbital ridge
11 arch 2 (A2)	0: separate from each other medially 1: fused medially
12 arch 5 (A5)	0: arch fused to pterotic 1: tube separate from pterotic
13 arch 6 (A6)	0: arch fused to parietal 1: tube separate from parietal
14 posterior tabular of pterotic	0: arch fused to pterotic 1: tube separate from pterotic
15 posterior supratemporal	0: present 1: absent

16	medial supratemporal	0: separate from post. tabular of pterotic 1: fused to posterior tabular of pterotic
17	medial supratemporal	0: separate from posttemporal 1: fused to posttemporal by ridge
18	operculomandibular canal	0: separate from Infraorbital canal 1: connected to Infraorbital canal
19	infraorbitals 1-3 (suborbitals)	0: arches without spines 1: arches bear spines
20	infraorbital 3	0: arches fused dorsally 1: arches separate
21	infraorbital stay (suborbital stay)	0: normal 1: very thin and long
22	infraorbitals 4, 5, and 6	0: all three present 1: two present, probably IO4 and IO6 2: one present, probably IO6
23	primary preopercular spines	0: present 1: absent
24	secondary preopercular spines	0: absent 1: present
25	coracoid	0: normal 1: truncate
26	coracoid-4th actinost	0: posterior notch 1: complete articulation
27	articulation of scapula on cleithrum	0: articulates dorsally and ventrally 1: articulates dorsally only
28	scapula-2nd actinost	0: articulates with scapula 1: does not articulate with scapula
29	actinost pores	0: present 1: absent
30	post cleithrum	0: 2 elements 1: 1 element 2: absent
31	pelvic girdle	0: triangular "normal cottid-like" 1: square shape anteriorly
32	stegural	0: present 1: absent
33	hypural-parahypural fusion	0: less than half 1: more than half

- | | | |
|----|-----------------------------|----------------------------------|
| 34 | branchiostegal
membranes | 0: joined
1: fused to isthmus |
| 35 | cirri | 0: present
1: absent |
| 36 | skin prickles | 0: present
1: absent |
| 37 | hyohyoides inferioris | 0: absent
1: present |

Appendix II

Character Matrix

Taxa abbreviations:

H. s., *Hexagrammus stelleri*; *C. r.*, *Cottus ricei*; *J. z.*, *Jordania zonope*; *D. s.*, *Dasycottus setiger*; *E. g.*, *Eurymen gyrinus*; *C. g.*, *Cottunculus granulatus*; *C. t.*, *Cottunculus thomsonii*; *A. a.*, *Ambophthalmos angustus*; *A. m.*, *Ambophthalmos magnicirrus*; *M. g.*, *Malacocottus gibber*; *M. k.*, *Malacocottus kincaidi*; *N. l.*, *Neophrynichthys latus*; *E. b.*, *Ebinania brephocephala*; *P. ph.*, *Psychrolutes phrictus*; *P. pa.*, *Psychrolutes paradoxus*; *P. s.*, *Psychrolutes sigalutes*.

Taxon	Character number																																						
	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3																																						
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7												
<i>H. s.</i>	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>C. r.</i>	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0				
<i>J. z.</i>	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>D. s.</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0			
<i>E. g.</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0	1	0		
<i>C. g.</i>	0	0	0	?	0	0	1	1	0	0	0	0	0	1	1	?	?	1	1	0	0	2	1	1	1	1	1	0	1	1	1	?	?	1	1	0	?		
<i>C. t.</i>	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	0	0	2	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	
<i>A. a.</i>	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1	0	
<i>A. m.</i>	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	?	?	?	?	?	?	?	?	1	1	1	1	0	1	0
<i>M. g.</i>	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	?	1	?	1	0	0	0	0		
<i>M. k.</i>	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	0	
<i>N. l.</i>	1	1	1	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	1	
<i>E. b.</i>	0	1	1	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	1	
<i>P. ph.</i>	1	1	1	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1	0	1	0	1	1	0	?	?	?	?	?	1	0	?	1	0	1	0	1	1	
<i>P. pa.</i>	1	1	1	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	1	1	1	1	0	0	0	1	0	1	2	1	1	0	1	1	1	1		
<i>P. s.</i>	1	1	1	0	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	1	0	1	2	1	1	0	1	1	1	1	